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# PALAEONTOGRAPHICA AMERICANA

VOL. VIII

1974-1978

PALEONTOLOGICAL RESEARCH INSTITUTION
Ithaca, N. Y. 14850 U.S.A.

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No separate index is included in the volume. Each number is indexed separately. Contents of the volume are listed in the beginning of the volume.

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# PALAEONTOGRAPHICA AMERICANA

(Founded 1917)

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No. 47

## A REVISION OF THE FAMILY SERAPHSIDAE (GASTROPODA: STROMBACEA)

By

PETER JUNG

1974

Paleontological Research Institution
Ithaca, New York, U.S.A. 14850

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November 25, 1974

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*Library of Congress Card Number: 74-77128*

Printed in the United States of America
Arnold Printing Corporation

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# A REVISION OF THE FAMILY SERAPHSIDAE (GASTROPODA: STROMBACEA)

Peter Jung
Naturhistorisches Museum, Basel
Switzerland

## ABSTRACT

*Terebellum* and its relatives are treated as an independent family within the superfamily Strombacea, and its species are revised taxonomically. The Seraphsidae are subdivided into the three genera *Seraphs* Montfort, 1810, *Paraseraphs,* new genus, and *Terebellum* Röding, 1798. The genus *Seraphs* is furthermore subdivided into the three subgenera *Seraphs s. str., Miniseraphs,* new subgenus, and *Diameza* Deshayes, 1865. *Seraphs* ranges from late Paleocene to Oligocene, *Paraseraphs* from early to late Eocene, and *Terebellum* from Miocene to Recent. *Paraseraphs* probably derived from *Seraphs* during late Paleocene or early Eocene times, whereas *Terebellum* appears to have been derived from an Oligocene or even younger species of *Seraphs s. str.* The subgenera *Miniseraphs* and *Diameza* represent a local offspring of *Seraphs s. str.* which lived during the middle Eocene. The distributional patterns of supraspecific groups during different times are shown on a series of maps. The following new taxa are described: *Paraseraphs,* n. gen.; *Miniseraphs,* n. subgen. of *Seraphs; Seraphs (Seraphs) leukoleptus,* n. sp., *S. (S.) mayeri,* n. sp., *Paraseraphs tetanus,* n. sp., and *P. placitus,* n. sp.

## ACKNOWLEDGMENTS

I am greatly indebted to the authorities of the Naturhistorisches Museum Basel for the use of all working facilities and for providing funds to visit museums and institutes in Geneva, Paris, London, Amsterdam, Leiden, and Brussels. Practically all photographs were taken by Mr. W. Suter, photographer at the Naturhistorisches Museum Basel, for whose thorough work I am very grateful. I am also obliged to Mr. O. Garraux, Basel, for the fine drawings of specimens.

It would have been impossible to gather the information contained in this paper without the help of many persons. I was fortunate enough to receive help in the form of photographs, artificial casts, specimens on loan, literature, and stratigraphic and taxonomic information from the following persons: C. O. van Regteren Altena, Rijksmuseum van Natuurlijke Historie, Leiden; H. E. Coomans, Zoölogisch Museum, Amsterdam; M. Glibert, Institut Royal des Sciences Naturelles, Brussels; G. E. de Groot, Rijksmuseum van Geologie en Mineralogie, Leiden; the late L. G. Hertlein, California Academy of Sciences, San Francisco; L. Hottinger, Geologisches Institut, Basel; H. Jäger, Paläontologisches Institut und Museum, Berlin; I. A. Korobkov, Leningrad; E. Lanterno, Muséum d'Histoire Naturelle, Geneva; P. Lemoine, Ecole des Mines, Paris; J. Manivit, Université d'Orsay, Paris; C. P. Nuttall, British Museum (Natural History), London; K. V. W. Palmer, Paleontological Research Institution, Ithaca, New York; J. H. Peck, University of California, Berkeley; E. S. Richardson, Field Museum of Natural History, Chicago; S. S. Sarkar, Geological Survey of India, Calcutta; M. V. A. Sastry, Geological Survey of India, Calcutta; A. M. Vergneau-Saubade, Muséum d'Histoire Naturelle, Bordeaux; H. Schaub, Naturhistorisches Museum, Basel; K. Schmidt, Zentrales Geologisches Institut, Berlin; D. L. F. Sealy, British Museum (Natural History), London; J. Sornay, Muséum National d'Histoire Naturelle, Paris; J. Villatte, Laboratoire de Géologie, Toulouse; F. Wiedenmayer, Naturhistorisches Museum, Basel; S. R. Windham, Florida Geological Survey, Tallahassee; W. P. Woodring, U.S. National Museum, Washington, D.C. To all of them I would like to express my sincere thanks.

## INTRODUCTION

The Seraphsidae were much more diversified and abundant in Paleogene times than during the Neogene. A study of fossil Seraphsidae must, therefore, start with Paleogene material. Material from the Eocene of the Paris Basin has proved to be the most useful for a start, not only because a number of species have been described from that area, but mainly because this material is usually excellently preserved and all morphological features can be studied. With a few exceptions the material, which I have seen from outside the Paris Basin, is preserved as internal casts. This circumstance often made identifications difficult or even impossible, and in many cases doubtful.

The interpretation of seraphsid steinkerns is partly responsible for excessive descriptive work and the introduction of many specific names by earlier authors. An example is provided by De Gregorio (1880, pp. 19-27), who probably did not study enough comparative material from the Eocene of the Paris Basin. A total of 76 specific names of Seraphsidae have been published. Of these only 23, *i.e.* not even a third, are considered as valid species. In addition to the 23 valid species three new species are described in this paper.

During this work I was fortunate enough to be able to use the collection of Mayer-Eymar which contains many species of Seraphsidae from all over the world. Mayer had labelled several species of "*Terebellum*" as new, but he never published those names (*e.g. T. archiaci* = "*T.*" *subconvolutus* and *T. gregorioi* = "*T.*" *mayeri,* n. sp).

In some of the synonymies and sometimes also in the text age indications are put in quotation marks. This appeared necessary in those cases, where there is no or not enough stratigraphic control.

The material figured in this paper is partly deposited in the Naturhistorisches Museum Basel (abbreviated NMB) together with numerous artificial casts of type and figured specimens housed at other institutions. Details as to repository can be found either in the text of the respective species and in the explanations of the plates.

## NOTES ON ECOLOGY

The only surviving species of the Seraphsidae, *Terebellum terebellum,* is a sand burrower. Its smooth, fusiform shell appears to be especially adapted for this mode of life. Even if completely buried the animal maintains contact with the space above the substrate by means of one of its two extensible eyestalks. The buried animal is covered by a layer of sand of about one centimeter thickness. The manner of moving forward in the substrate was described by D. P. Abbott (1962), and hypothetical drawings of the locomotion were given by Jung and Abbott (1967, pl. 318).

Living *T. terebellum* Linné seems to prefer a bottom of silt, sand, or mud between some coral, rock, and patches of algae. It has been collected dead from about one meter down to 100 meters, and live specimens have been recovered from low tide to a depth of 36 meters. According to D. P. Abbott (1962) *T. terebellum* is probably a herbivore like species of *Lambis* and *Strombus,* "feeding on small algae, algal detritus, and plant-like microorganisms".

Fossil species of Seraphsidae most frequently occur in calcareous sandstone, siltstone, or sandy, impure limestone, but they are rare in limestones. It appears, therefore, that fossil representatives of the Seraphsidae essentially had the same mode of life as the single, living species. From the nature of the sediments containing fossil seraphsids and the faunistic assemblages associated with them it is evident that they had a bathymetric range similar to that of the Recent species.

As pointed out by Jung and Abbott (1967, p. 446) the posterior end of the mantle edge of living *T. terebellum* "is modified into three appendages, two of them being short filaments. The third is extremely long and forms the deep sutural gutter almost all the way to the apex of the shell. We presume that this exposed filament is tactile in function and serves to inform the animal whether the shell is fully buried or not". In the genera *Seraphs* and *Paraseraphs* (and also in *Terebellopsis, Semiterebellum,* and *Mauryna*) there is no sutural gutter comparable to that of *Terebellum.* Perhaps the posterior canal of *Paraseraphs* (and *Terebellopsis, Semiterebellum,* and *Mauryna*) was occupied by a similar filament serving the same function. In *Seraphs* this filament may have been situated in the slit between the adapical end of the aperture and the apex. In the middle Eocene *S. chilophorus* Cossmann this filament may have been unusually long giving rise to the development of a short "apical canal" (see Text-figure 16).

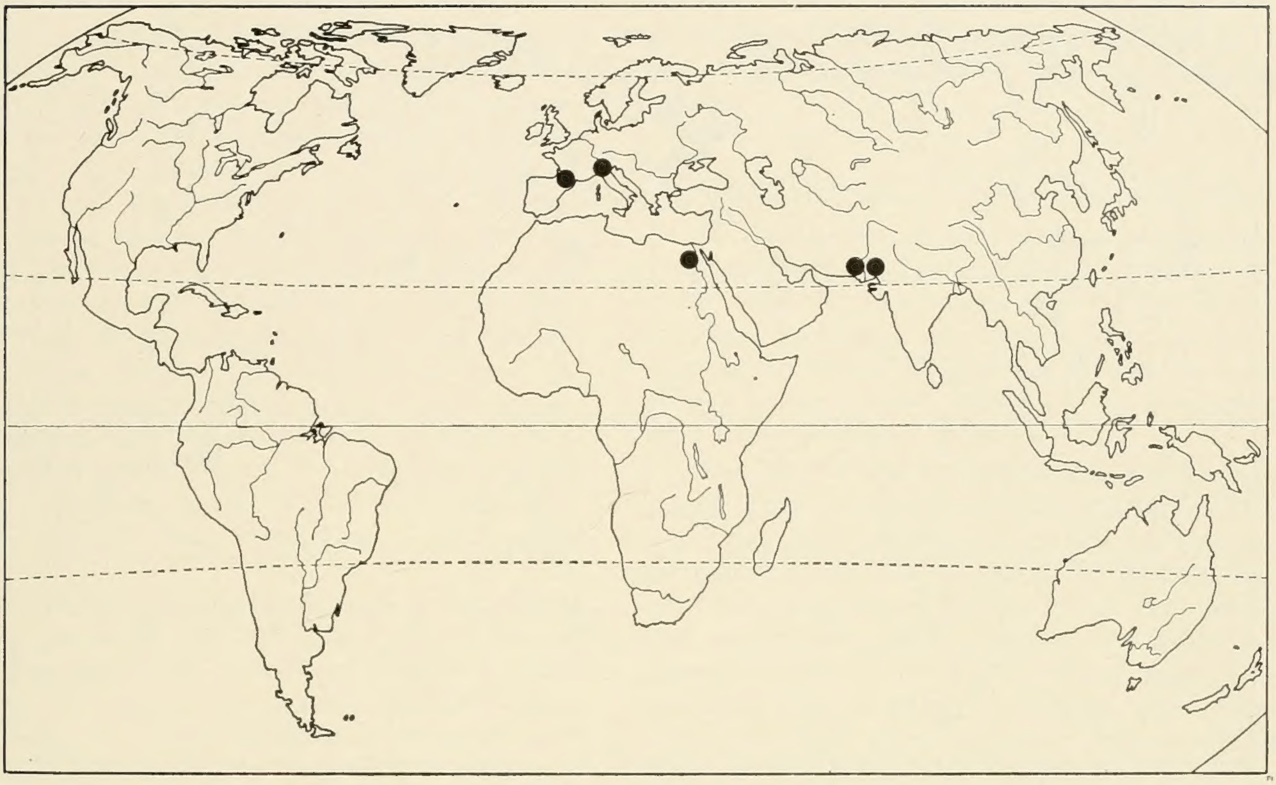
## HORIZONTAL AND VERTICAL DISTRIBUTION OF SUPRASPECIFIC GROUPS

The Seraphsidae were distributed all over the Tethys at one stage or another of their history. But the different genera show different distributional patterns which in turn were changing through time. The distributional maps here presented may well be subjected to modifications as more material and more precise stratigraphic information becomes available.

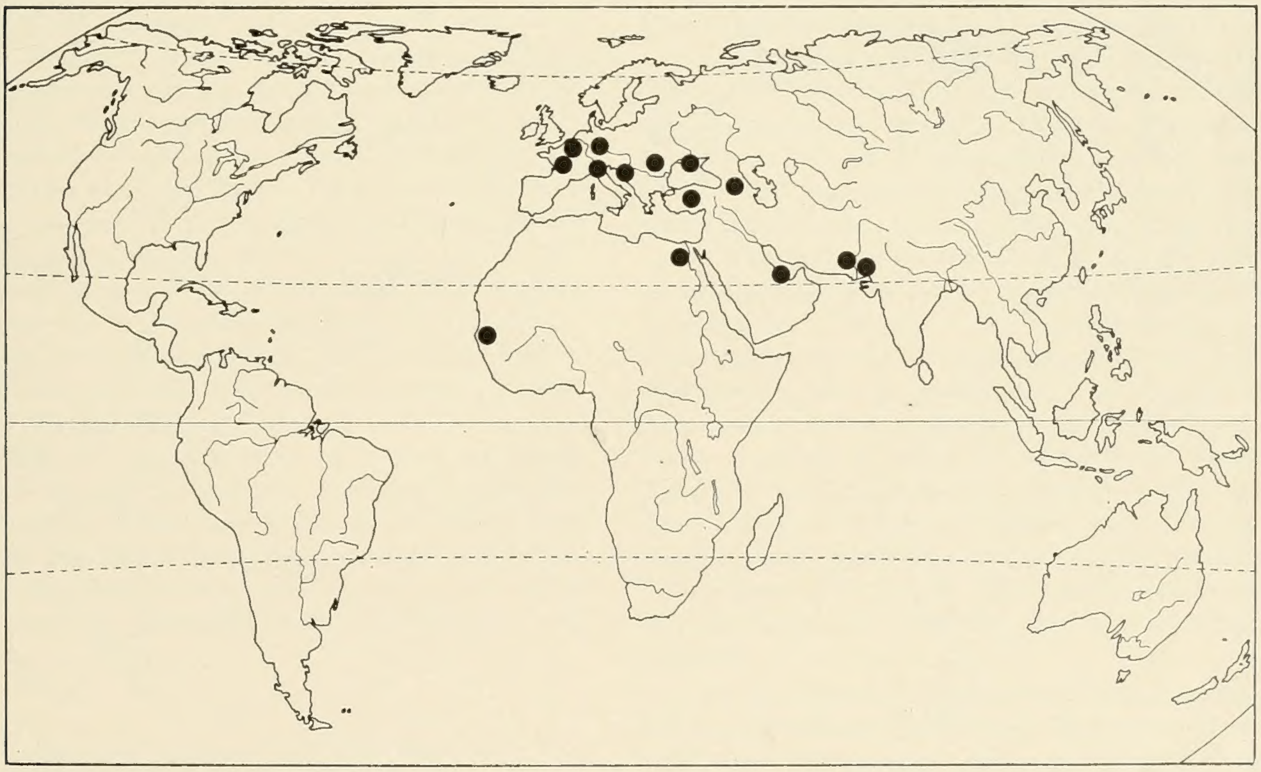
The distribution of the subgenus *Seraphs* at different times is shown in Text-figures 1 to 4. According to published records *Seraphs s. str.,* the oldest subgenus of the family, apparently came into existence in southern France during late Paleocene times. From there it spread over parts of Europe and eastward as far as Egypt, Pakistan, and northwestern India. Early Eocene records of *Seraphs s. str.* are rare, but during middle Eocene times it not only developed a great morphological diversity but also occurred in great numbers at certain localities (Paris Basin, northern Italy, Rumania, Egypt). During the late Eocene the subgenus spread far eastward (Java) and westward (Central America, Florida), and its Oligocene distribution looks like a relic.

Representatives of the subgenera *Miniseraphs* and *Diameza* are rare. Stratigraphically they are restricted to the middle Eocene. *Seraphs (Diameza) intermedius,* the only species of the subgenus, has so far been found in the Paris Basin only, whereas one of the two species of *Miniseraphs* is recorded from the Paris Basin, northern Italy, and Hungary.

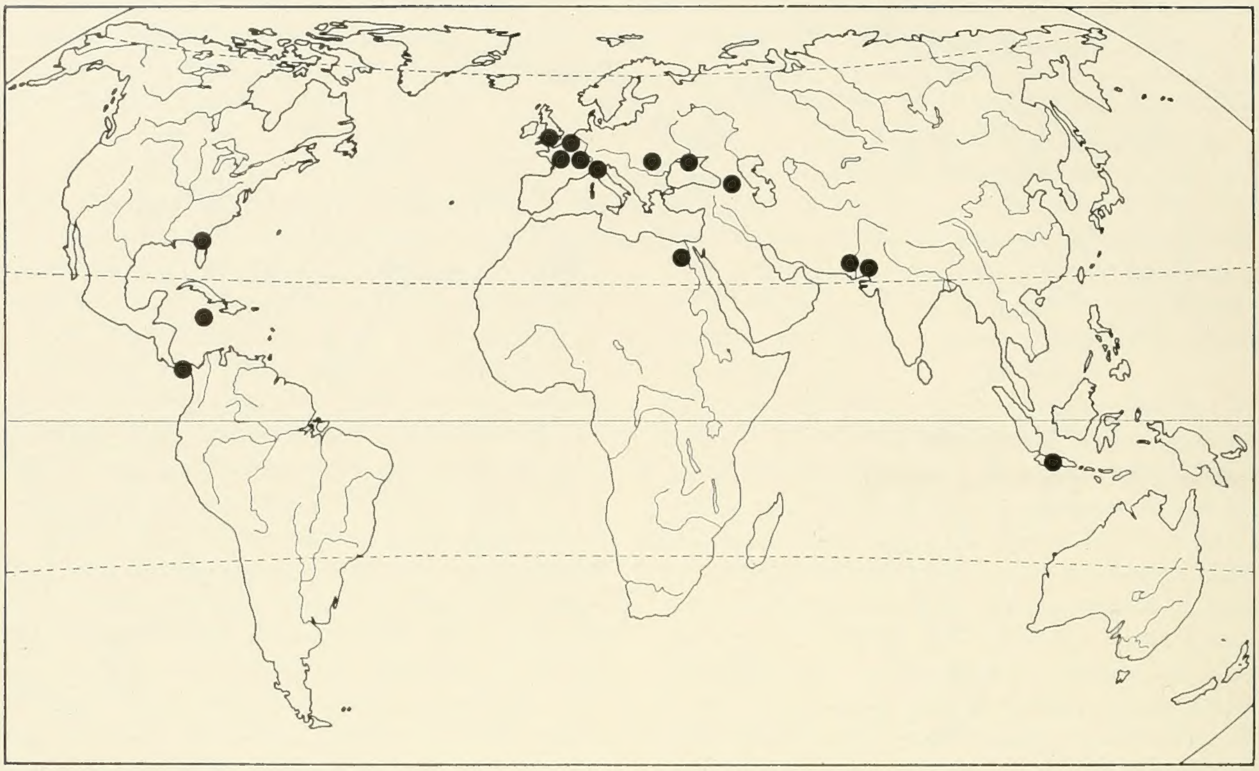
Five records, which would modify the distribution maps considerably, are omitted due to lack of taxonomic or stratigraphic information. The first is *S. minus* (Vincent) from the Paleocene (?) of Cabinda, Angola. The second is an unpublished occurrence of *S. sopitus* (Solander) in an unspecified Eocene horizon (possibly middle Eocene: see Doncieux, 1948) of an unspecified locality in Madagaskar (collection of the Muséum National d'Histoire Naturelle Paris, No. B 23194). The third is an unidentified species of "*Terebellum*" from the Eocene of Texas reported upon by Harris (1890, p. 315), and listed by Palmer and Brann (1966, p. 946) as *Terebellum* sp. from the middle Eocene Reklaw Formation of Texas. The fourth concerns *Terebellum fusiforme* Lamarck as published by De Gregorio (1890, p. 116, pl. 10, figs. 7-10). De Gregorio's material is not identifiable but possibly represents a species of *Para-*



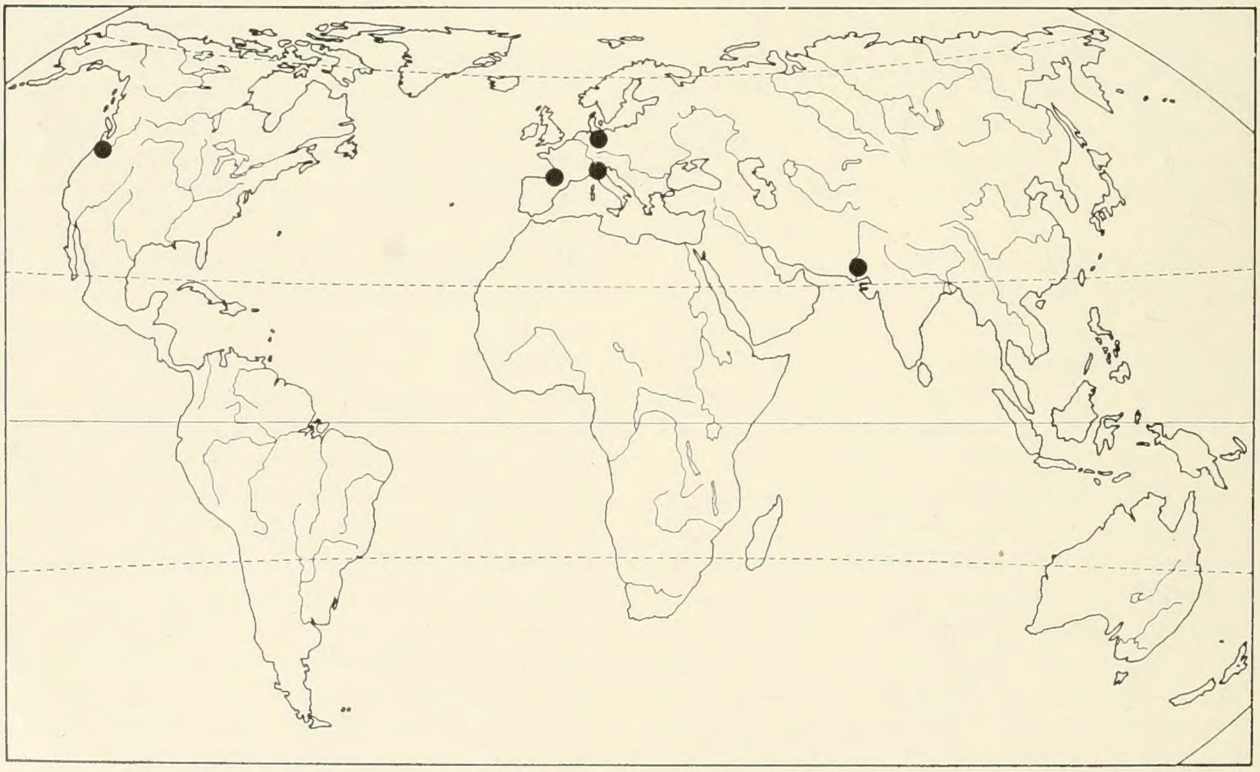
Text-figure 1. Distribution of *Seraphs s. str.* during late Paleocene and early Eocene times.



Text-figure 2. Distribution of *Seraphs s. str.* during the middle Eocene.



Text-figure 3. Distribution of *Seraphs s. str.* during the late Eocene.



Text-figure 4. Distribution of *Seraphs s. str.* during the Oligocene.

*seraphs*. According to Richards and Palmer (1953, p. 25) it was probably collected from beds of late Eocene age, and Palmer and Brann (1966, p. 946) listed it as *Terebellum* sp. The fifth record, which has been omitted from the distribution maps, concerns an unpublished, silicified specimen of "*Terebellum*" from the early Miocene Tampa Limestone of Florida, which was said to be in the Tucker collection (formerly Chicago Natural History Museum) and was collected by Druid Wilson of the U.S. Geological Survey at locality 57 (Sixmile Creek). According to written communication from Dr. E. Richardson of the Field Museum of Natural History it has not been possible to locate this specimen. This specimen is of considerable interest, because it would represent the youngest record of the family from America and Europe. If it really is a seraphsid, it almost certainly is a species of *Seraphs* or *Paraseraphs* and not a *Terebellum*, because true *Terebellum* never reached America.

The distribution of *Paraseraphs* is shown in Text-figures 5 to 7. The genus appeared during the early Eocene of France and northern Italy. Text-figure 5 shows an early Eocene record in Jamaica. This record is somewhat doubtful as it is based on a single, insufficiently preserved, internal cast from the early Eocene Richmond Formation of eastern Jamaica, which is identified as *Paraseraphs* ? sp. During the middle Eocene, however, *Paraseraphs* certainly reached the Caribbean and California, and *P. procerus* is even most abundant in the middle Eocene Chapelton Formation of Jamaica. During the late Eocene *Paraseraphs* spread more in the Western Hemisphere reaching Panamá, Trinidad, and Florida, whereas in the Old World it does not occur farther east than Egypt. There are no Oligocene records of *Paraseraphs, i.e.* the genus apparently became extinct at the end of the Eocene.

The distribution of *Terebellum* is shown in Text-figure 8. The broken line encloses the distribution of Recent occurrences (see also Jung and Abbott, 1967, pl. 327).[1] It may be noted at this point that the distribution areas of *Paraseraphs* and *Terebellum* do not overlap.

Text-figure 9 is an attempt of an indirect correlation of the ranges of selected Paleogene species of Seraphsidae with the succession of planktonic foraminiferal biozones. It is based on the correlation of seraphsid localities with nummulitid and alveolinid biozones which in turn are correlated with the planktonic foraminiferal zones (Hottinger and Schaub, 1960; Hottinger, Lehmann, and Schaub, 1964; Hottinger, 1971). Text-figure 9 has been prepared in cooperation with L. Hottinger, whose help is gratefully acknowledged.

## EVOLUTIONARY TRENDS AND PHYLOGENY

No attempt is made to trace phylogenetic relationships at the specific level. This would be a hopeless undertaking at this stage, not only because there are too many gaps in the fossil record, but also because there is not enough stratigraphic control in many cases. In addition a large percentage of the available material is in an unsatisfactory state of preservation.

The genera of the Seraphsidae can be divided into two groups. The evolute group comprises the genera *Terebellum* and *Paraseraphs*, and the involute group is represented by the genus *Seraphs*. The two groups are phylogenetically related. Jung and Abbott (1967, p. 450, pl. 326) distinguished four stages during the ontogenetic development of the Recent *T. terebellum*: 1. the protoconch stage, 2. the first terebelloid stage, 3. the seraphoid stage, and 4. the second terebelloid stage. In other words: evolute and involute stages are succeeding each other during ontogeny. A similar situation can be observed in immature specimens of *Paraseraphs tetanus*, n. sp. which also show evolute and involute stages (see Pl. 9, fig. 26, and Text-figures 26, 27).

The involute coiling of the shell as represented by *Seraphs* was the dominant form during the Paleogene history of the family, whereas in Neogene times only evolute forms occur. *Seraphs s. str.* appeared first and gave rise to all the other supraspecific groups of the family (see Text-figure 10). *Seraphs s.l.* consists of at least 15 species, whereas in *Paraseraphs* only 6 species are recognized. *Paraseraphs* is characterised by its slender shape and the posterior canal. Some species of *Seraphs s. str.*, however, show a clear tendency toward the main characteristics of *Paraseraphs*. Thus the middle Eocene *S. leukoleptus*, n. sp., has the fusiform, slender shape of species of *Paraseraphs*, but it is entirely involute as species of *Seraphs* (Text-figure 17). On the other hand the middle Eocene *S. chilophorus* has the typical general shape of species of *Seraphs*, but it has an "apical canal" which looks like a rudimentary posterior canal (Text-figure 16). In the Oligocene *S. mayeri* the shell material behind its "posterior canal" is sometimes partly resorbed.

All the features just mentioned demonstrate the close relationship between *Seraphs* and *Paraseraphs*. On the other hand two of the youngest species of *Seraphs* show what ap-

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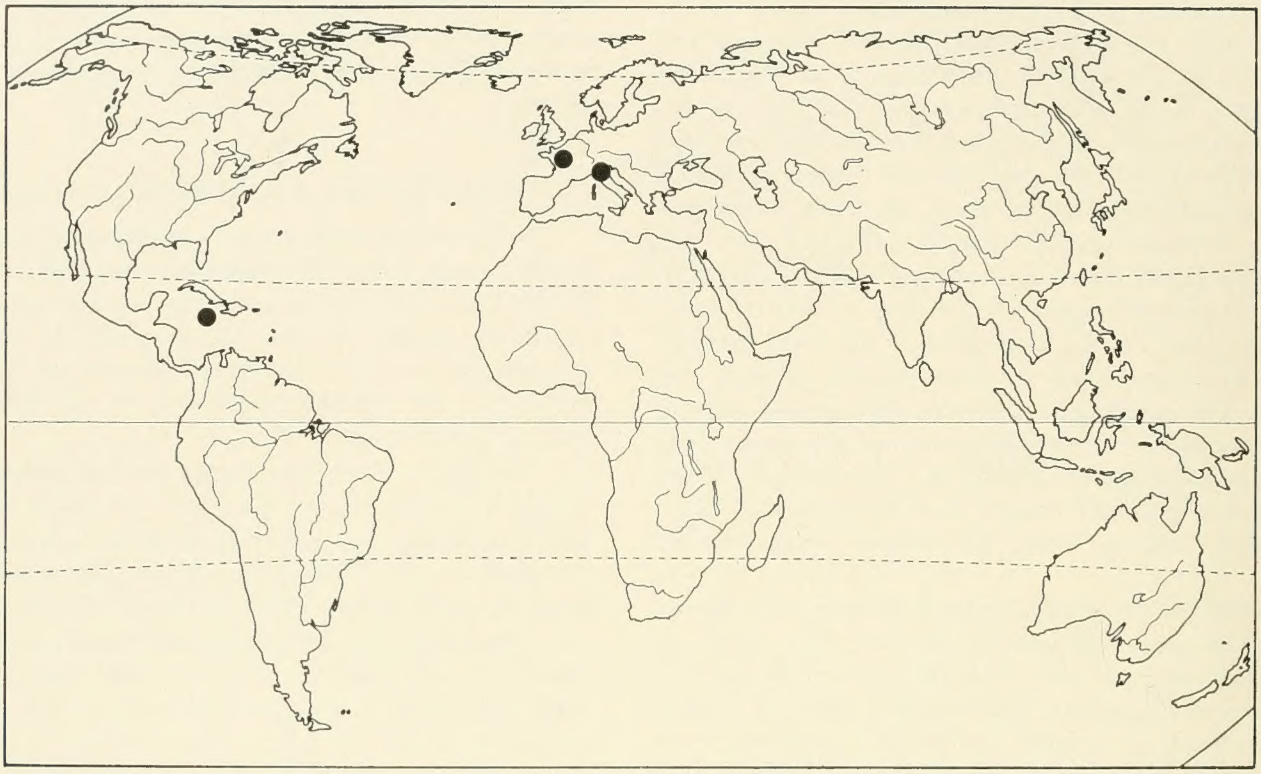
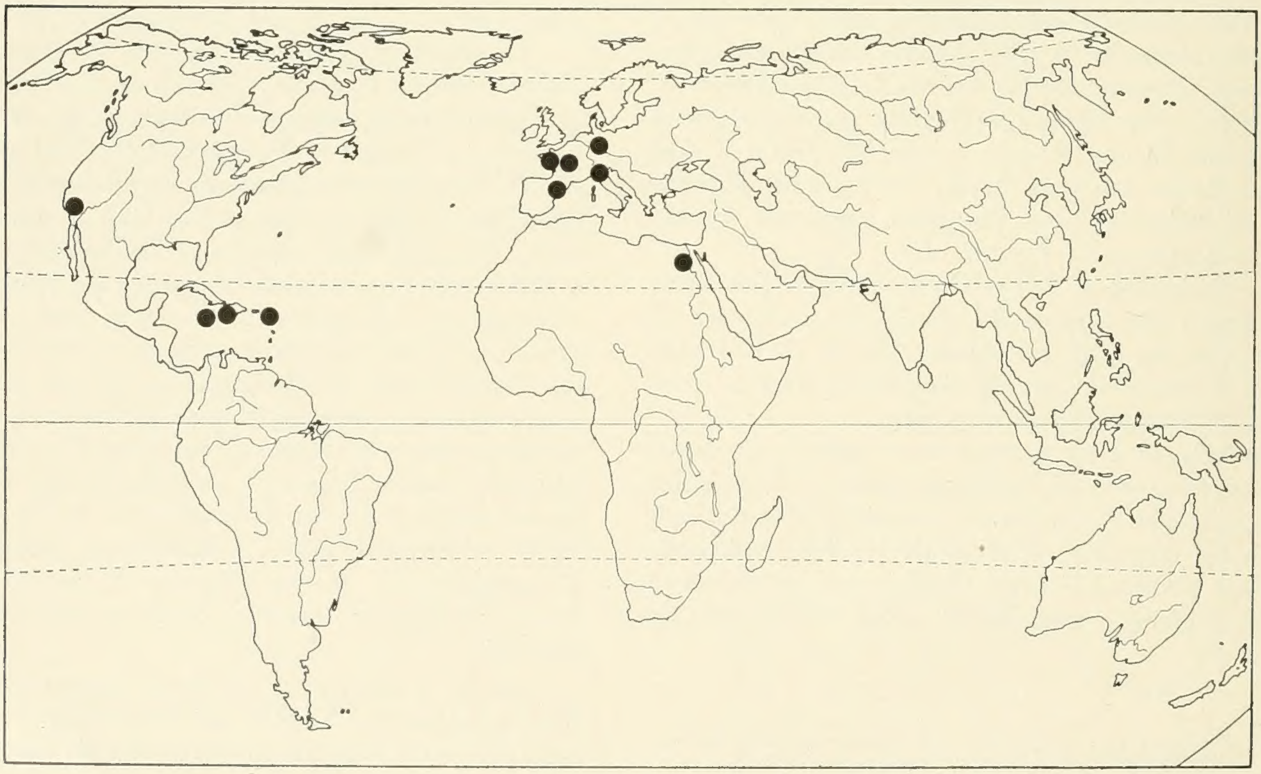
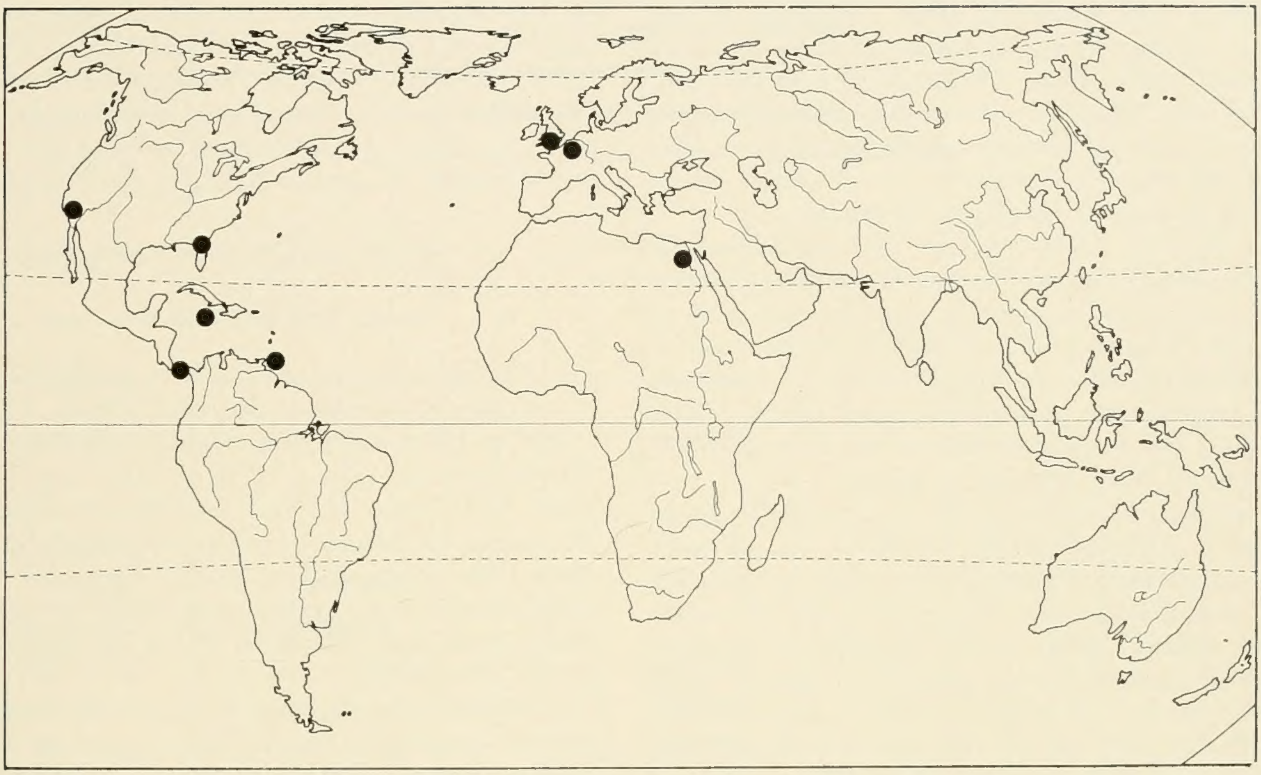
[1] After Text-figure 8 was prepared a new Recent record in the Persian Gulf came to my attention (Biggs, 1973, p. 364).



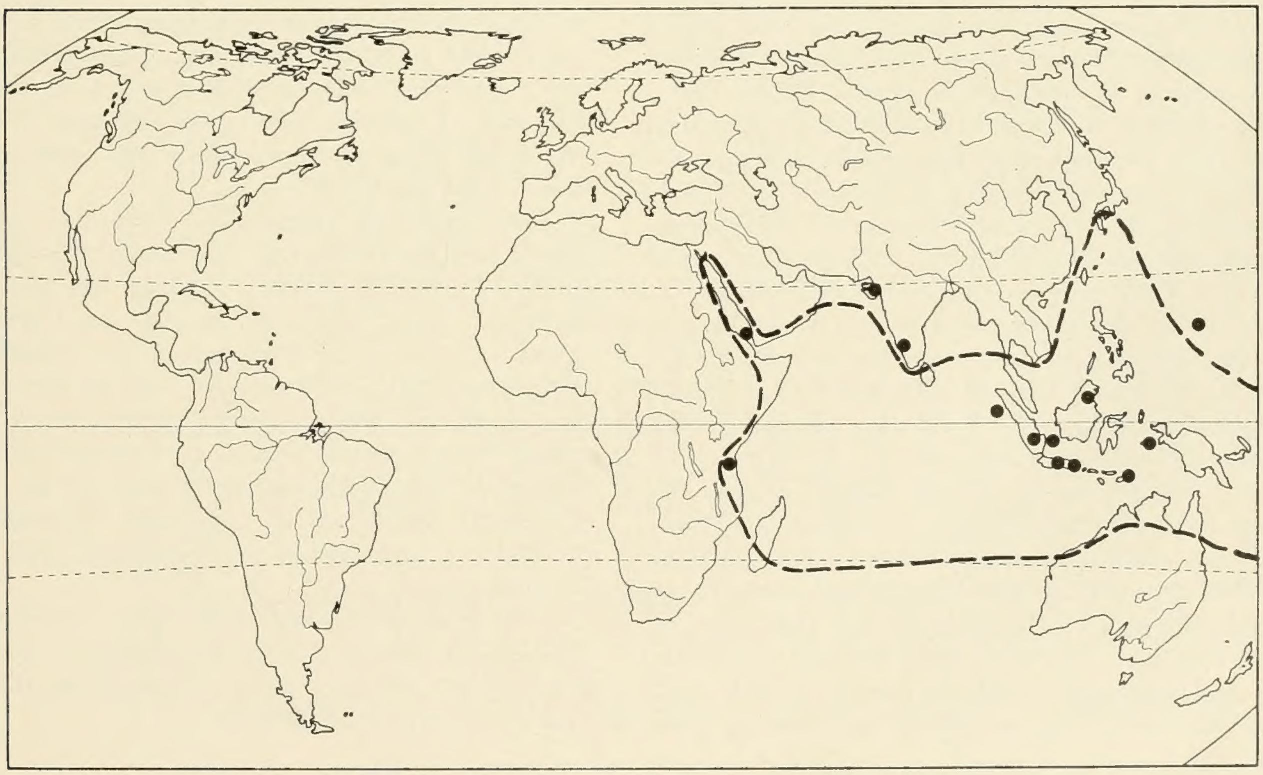
Text-figure 5. Distribution of *Paraseraphs* during the early Eocene.



Text-figure 6. Distribution of *Paraseraphs* during the middle Eocene.



Text-figure 7. Distribution of *Paraseraphs* during the late Eocene.



Text-figure 8. Distribution of *Terebellum* from Miocene to Pleistocene times. Broken line: distribution of Recent *T. terebellum*.

pears to be a trend toward the genus *Terebellum*. *S. subconvolutus* (d'Orbigny) from the Stampian of the Aquitaine Basin, France, and *S. naricus* (Vredenburg) from the Stampian of Pakistan, both have a slender shape and opisthocline growth lines above the adapical end of their apertures. This latter feature looks like a tendency toward evolute coiling of the shell as shown by species of *Terebellum*.

It is, therefore, highly probable that the ancestor of *Terebellum* lived in the late Oligocene of the India-Pakistan area and southeast of it. However, there are no records of late Oligocene seraphsids, and the earliest records of species of *Terebellum* are dated as early Miocene (*T. terebellum* from the early Miocene of Saipan, Mariana Islands (Ladd, 1972, p. 57), and *T. cinctum* Martin and *T. papilliferum* Martin from the "early Miocene" of Java).

The phylogenetic relationships of supraspecific groups are indicated in Text-figure 10. *Seraphs s. str.* appeared first, but its ancestry is uncertain. It cannot be excluded, however, that *Seraphs s. str.* derived from *Semiterebellum* Cossmann. Villatte (1962, p. 211) described *S. leymeriei* from beds in southern France, which she originally dated as Montian but later as early Thanetian (Tambareau and Villatte, 1968, p. 58), and the type species of *Semiterebellum, S. marceauxi* Deshayes, occurs in the Thanetian of the Paris Basin. Whatever species the actual ancestor of the first seraphsid was, it is possible that the family originated in France, from where it spread to east and west. The family became more diversified and spread over large areas during the early Eocene; it flourished in middle Eocene times, when the subgenera *Miniseraphs* and *Diameza* came into existence. These two subgenera represent local, rather unsuccessful offsprings of *Seraphs s. str.* Specimens of their species are rare, and they are restricted in time to the middle Eocene. That the Seraphsidae had reached their acme of diversity and development during the middle Eocene is also shown by the fact that some of its species grew to unusually large dimensions. Large specimens of *S. sopitus* (Solander) for instance occur in great numbers at certain middle Eocene localities in the Paris Basin, the Cluj Basin (Rumania), and in Egypt, and some of these large individuals survived the middle Eocene ranging up into the late Eocene. Another large seraphsid is *Paraseraphs procerus* (Merian), which is most abundant at some localities of the middle Eocene Chapelton Formation of Jamaica.

Already during late Eocene times but even more so during the Oligocene there was a rapid decline as to species diversity and abundance until the genera *Seraphs* and *Paraseraphs* became extinct. As already mentioned there are no late Oligocene records of seraphsids. However, the family survived the Paleogene and continued to live in the Neogene, where species of the genus *Terebellum* first appeared. But *Terebellum* never evolved into a flourishing group, and it looks as though the history of *Terebellum* and its species would confirm the general decline of the Seraphsidae.

## SYSTEMATIC DESCRIPTIONS

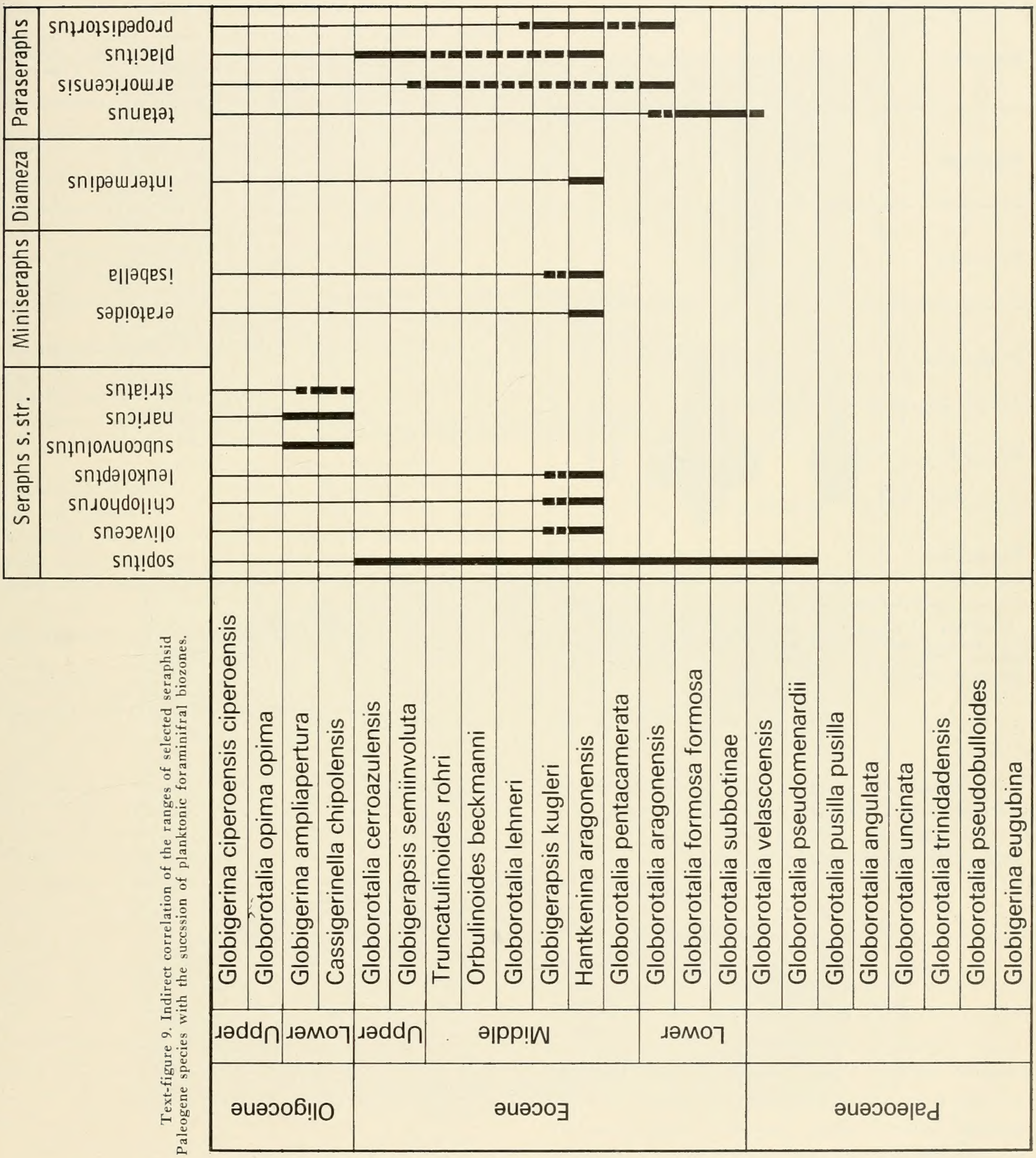
### Family **SERAPHSIDAE**, new name

*Terebellum* and its relatives have usually been assigned to the family Strombidae. However, already De Gregorio (1880, p. 19) grouped them together under the subfamily Terebellinae and Sacco (1893, p. 21) used the family name Terebellidae. This fact has either not been accepted by western workers, or it has been overlooked. On the other hand some eastern workers followed Sacco and considered the Terebellidae as an independent family within the superfamily Strombacea (Mészáros, 1957, p. 44; Bagmanov, 1966, p. 178; and others).

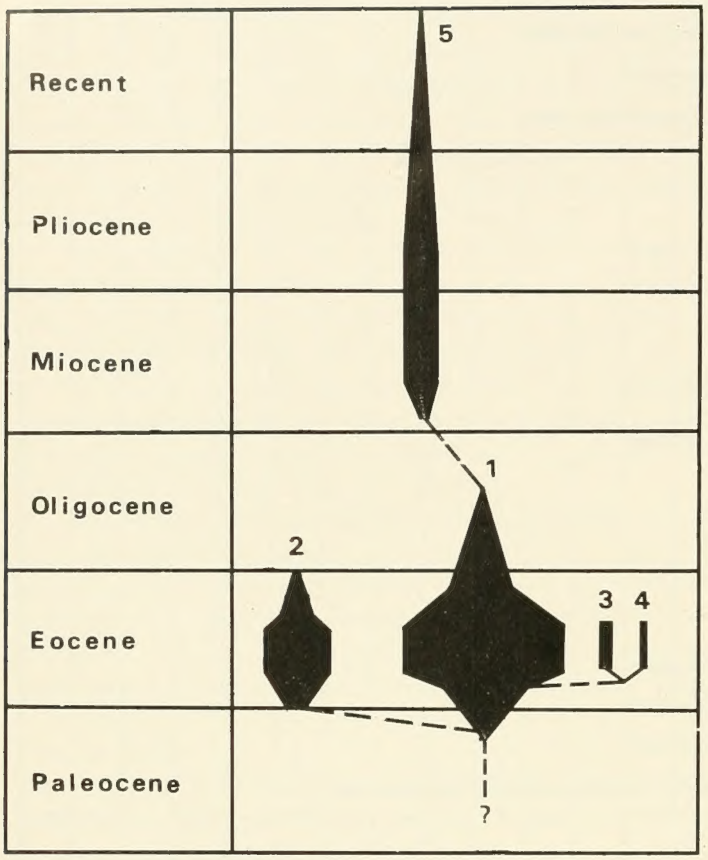
All these authors obviously considered *Terebellum* as the type genus of the family. Unfortunately the name Terebellidae is preoccupied by the polychaete family Terebellidae, the type genus of which is *Terebella* Linné, 1767. Grube (1851, the two tables in front of p. 281, pp. 281, 325) called the family Terebellacea and Malmgren (1868, p. 216) Terebellidae. The polychaete family name has, therefore, priority, and the gastropod family needs a new name and another type genus. I herewith select *Seraphs* Montfort, 1810, as the type genus of the gastropod family and derive the family name Seraphsidae from it.

The stromboid affinities of *Terebellum* are demonstrated by the operculum and the radula of its Recent type species, *Terebellum terbellum* (Linné) (see Abbott, 1960; Jung and Abbott, 1967). On the other hand there is good reason to separate the three genera here included in the Seraphsidae from the Strombidae: they all lack the stromboid notch (*i.e.* it is not developed as a notch; the basal margin of the body whorl simply does not reach down to the level of the base of the columella), and they are (with few exceptions) devoid of any sculpture. Strombid genera usually have some kind of spiral sculpture, axial swellings, or spines.

The stratigraphic range of the family as a whole is from Paleocene to Recent, but the morphological diversity and frequency of occurrence is not uniform during this interval (see above and Text-figure 10).



Text-figure 9. Indirect correlation of the ranges of selected seraphsid Paleogene species with the succession of planktonic foraminifral biozones.



Text-figure 10. Stratigraphic ranges of seraphsid genera and subgenera showing possible phylogenetic relationships and relative abundance of their species. 1. *Seraphs s. str.* 2. *Paraseraphs* 3. *Miniseraphs* 4. *Diameza* 5. *Terebellum.*

The Seraphsidae comprise the three genera *Seraphs, Paraseraphs,* and *Terebellum.* Their most diagnostic, morphological features are tabulated below, and the type species of each genus is illustrated for comparison in Text-figures 11 to 13.

| | coiling | posterior canal | outer lip | channelled suture | maximum diameter |
|---|---|---|---|---|---|
| *Seraphs* | involute | absent | undulating | absent | at about middle of height |
| *Paraseraphs* | evolute | present | prosocyrt | absent | near base |
| *Terebellum* | evolute | absent | prosocyrt | present | near base |

## Genus SERAPHS Montfort

*Seraphs* Montfort, 1810, Conchyliologie systématique, vol. 2, pp. 374 (fig.) 375 (type: *Seraphs convolutus* Lamarck); Wenz, 1938-1944, Handbuch der Paläozoologie, Bornträger, Berlin, vol. 6, pt. 4, p. 938, 1940 (type: *Terebellum convolutum* Lamarck).

*Seraps* Férussac, 1822, Tableaux systématiques des animaux mollusques . . ., p. xxxvi.

*Seraphe* Blainville, 1825-1827, Manuel de malacologie et de conchyliologie, p. 416, 1825 (type by monotypy: *Terebellum convolutum* Lamarck).

*Seraphys* Gray, 1841, Synopsis of the contents of the British Museum, ed. 43, p. 124. Gray, 1842, *ibidem,* ed. 44, pp. 52, 89.

*Serapis* Link, 1830, Handbuch der physikalischen Erdbeschreibung, pt. 2, p. 441.

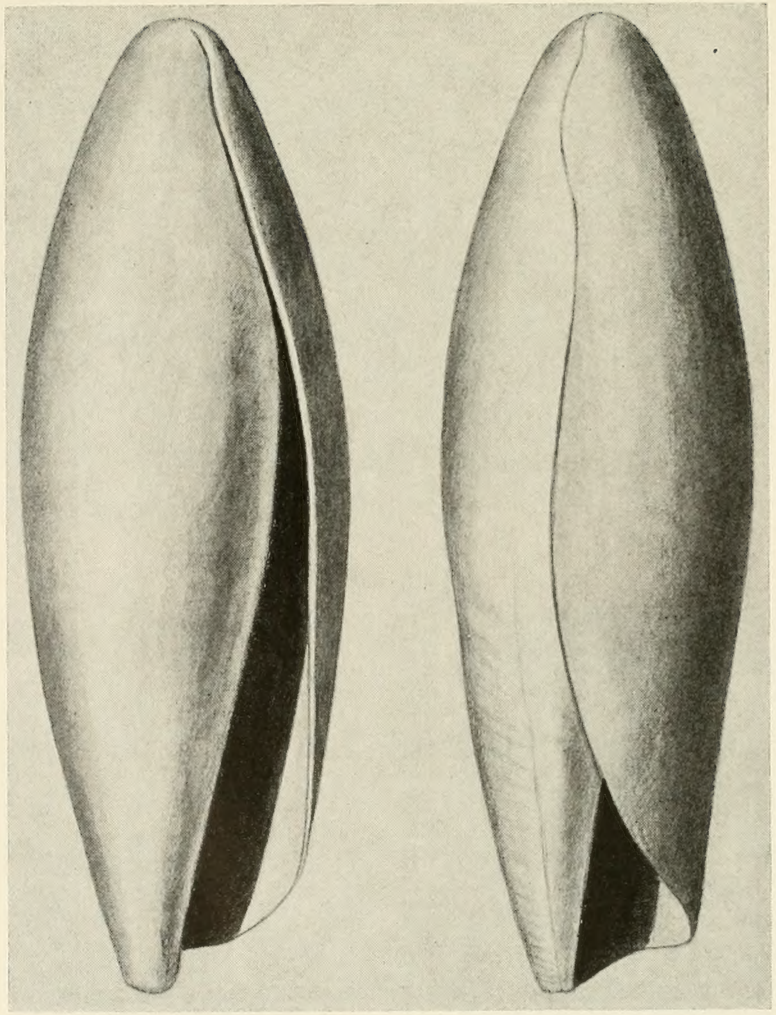
Type species (by original designation): *Seraphs convolutus* Lamarck (= *Terebellum convolutum* Lamarck, 1802 = *Bulla sopita* Solander, 1766). Late Paleocene to late Eocene, Europe.

*Description.* — Shell small to large, moderately slender, smooth, involute. Callus on inner lip thin. Growth lines undulating, *i.e.* prosocyrt on lower half of shell, followed adapically by an opisthocyrt and then again a prosocyrt portion. Largest diameter of shell near the middle of the height of the shell. Outer lip not thickened.

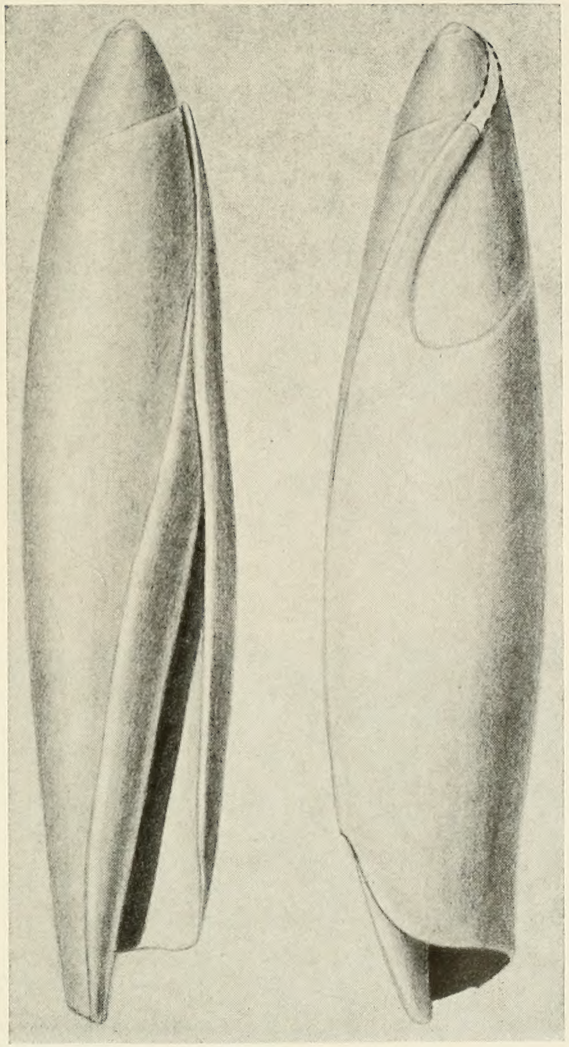
The genus *Seraphs s.l.* comprises at least 15 species and is thus the most diversified genus of the family. On one hand the genus includes small forms such as the species of the subgenera *Miniseraphs* and *Diameza,* but on the other hand *S. sopitus,* the type species of the genus, may reach large dimensions.

*Range.* — Paleocene to Oligocene. The ranges of the species of *Seraphs s.l.* are summarized below:

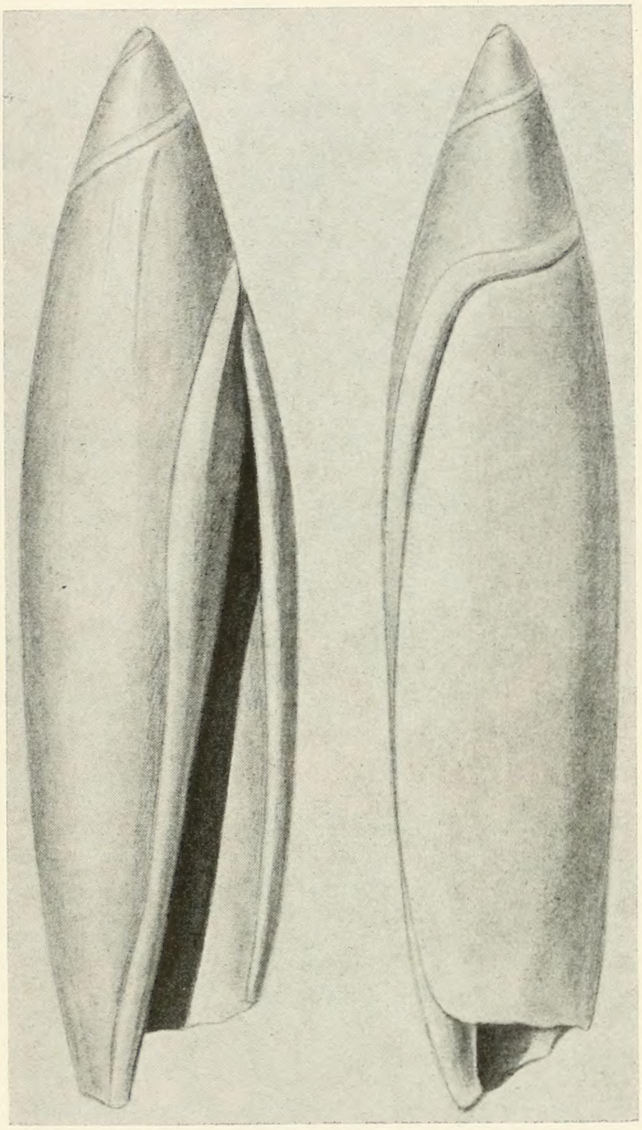
| | Paleocene | early Eocene | middle Eocene | late Eocene | Oligocene |
|---|---|---|---|---|---|
| *S. sopitus* | — — —— | ——— | ——— | ——— | |
| *S. olivaceus* | | | ——— | | |
| *S. chilophorus* | | | ——— | | |
| *S. leukoleptus* | | | ——— | | |
| *S. plicifer* | | | ——— | | |
| *S. minus* | ? ? | | | | |
| *S. belemnitus* | | | | ——— | |
| *S. squamosus* | | | | ——— | |
| *S. subconvolutus* | | | | | —— — — |
| *S. mayeri* | | | | | - —— — |
| *S. naricus* | | | | | ——— |
| *S. striatus* | | | | | —— — |
| *S. andersoni* | | | | | —— — |
| *S. eratoides* | | | ——— | | |
| *S. isabella* | | | ——— | | |
| *S. intermedius* | | | ——— | | |



Text-figure 11. Two views of a virtual topotype of *Seraphs sopitus*, the type species of *Seraphs s str.* NMB No. H 15406. Barton, Hants. Barton beds (upper Eocene); 5 ×.



Text-figure 12. Two views of a paratype of *Paraseraphs tetanus*, the type species of *Paraseraphs*. NMB No. H 15405. Cuise-Lamotte. Cuisian (early Eocene); 5 ×



Text-figure 13. Two views of *Terebellum terebellum,* the type species of *Terebellum..* NMB No. H 16599. Recent, Salomon Ids. Color pattern omitted; 5 ×.

## Subgenus **SERAPHS** s. str.

### **Seraphs (Seraphs) sopitus** (Solander)

Plate 1, figures 1-19; Plate 2, figures 1-8; Plate 3, figures 1-9; Plate 4, figures 1-13; Text-figure 11

*Bulla sopita* Solander, 1766, *in* Brander, Fossilia hantoniensia. London; p. 19, pl. 1, fig. 29a. (Late Eocene, southern England).

*Terebellum sopitum* Brander, d'Orbigny, 1850-1852, Prodrome de paléontologie . . ., vol. 2, p. 352, 1850; Deshayes, 1864-1865, Description des animaux sans vertèbres découverts dans le bassin de Paris, vol. 3, p. 469, 1865; Mayer, 1866, Vierteljahrsschrift Naturf. Ges. Zürich, Jg. 11, pp. 319, 333; Pavay, 1873, Mitt. königl. ungar. geol. Anstalt, vol. 1, pt. 3, pp. 363, 412 (Eocene, Rumania); Vasseur, 1881, Recherches géologiques sur les terrains tertiaires de la France occidentale. Stratigraphie. Première partie: Bretagne. Paris, pp. 174, 245, 267 (late middle Eocene, northwestern France); Oppenheim, 1894, Zeitschrift deutschen geol. Ges., vol. 46, p. 438; Oppenheim, 1896, Palaeontographica, vol. 43, p. 194 (early Eocene, northern Italy); Oppenheim, 1896, Zeitschrift deutschen geol. Ges., vol. 48, p. 71; Vinassa de Regny, 1898, Palaeont. Italica, vol. 3, pp. 147, 158.

*Terebellum sopitum* Solander, Newton, 1891, British Oligocene and Eocene Mollusca . . ., p. 98; Koch, 1894, Mitt. Jb. königl. ungar. geol. Anstalt, vol. 10, p. 277 (middle Eocene, Cluj basin, Rumania); Vinassa de Regny, 1896, Palaeont. Italica, vol. 1, pp. 223, 230, 260; Oppenheim, 1906, Palaeontographica, vol. 30, 3. Abt., 2. Lief., p. 298, pl. 25, fig. 13; Fabiani, 1915, Mem. Ist. Geol. Univ. Padova, vol. 3, pp. 143, 255, 261; Cuvillier, 1930, Mém. Inst. Egypte, vol. 16, pp. 79, 157, 253 (lower, middle, and upper Eocene of Egypt); Gabrielian, 1964, Paleogene and Neogene of the Armenian SSR (in Russian), Yerevan, p. 63, pl. 1, fig. 2 (upper Eocene, Armenia).

*Terebellum sopitum* (Solander), Cossmann, 1897, Bull. Soc. Sci. Nat. Ouest de la France, vol. 7, fasc. 4, p. 341, pl. 7, fig. 35 (middle Eocene, northwestern France); Vasilenko, 1952, Stratigraphy and molluscan fauna of the Eocene deposits of the Crimea (in Russian), VNIGRI, Leningrad-Moscow, p. 101, pl. 8, fig. 5 (upper Eocene, Crimea).

*Terebellum (Seraphs) sopitum* Solander, Dainelli, 1904, Palaeont. Italica, vol. 10, p. 162; Dainelli, 1905, Palaeont. Italica, vol. 11, pp. 75, 92 (middle Eocene, Jugoslavia); Doncieux, 1908, Ann. Univ. Lyon, n. s., I. Sci., Méd., fasc. 22, p. 92, pl. 4, fig. 15 (late Paleocene, southern France); Isaeva, 1933, Trans. United Geol. Prosp. Service USSR, fasc. 305, p. 31, pl. 3, fig. 11 (upper Eocene, Georgia, USSR). Mészáros, 1957, Mon. Geol. Paleont. (Ed. Acad. Rep. Pop. Rumania), No. 1, pp. 44, 143, pl. 8, fig. 7, pl. 28, figs. 4, 4a (middle and upper Eocene of Cluj basin, Rumania); Gabrielian, 1964, Paleogene and Neogene of the Armenian SSR (in Russian). Yerevan, pp. 78, 81 (upper Eocene and "early to middle Oligocene", Armenia). Bagmanov, 1966, Larger Foraminifera and mollusk fauna of the Eocene deposits of the Trans-Caucasus (in Russian). Baku, p. 180, pl. 81, figs. 11-17, pl. 82, figs. 4-6 (middle Eocene, Trans-Caucasus).

*Terebellus (Seraphs) sopitum* (Solander), Cossmann, 1889. Ann. Soc. Roy. Malac. Belgique, vol. 24, p. 96; Cossmann and Pissarro, 1899-1904, Bull. Soc. géol. Normandie, vol. 20, p. 89, pl. 15, fig. 5, 1900.

*Bulla volutata* Solander, 1766, *in* Brander, Fossilia hantoniensia. London; p. 34, pl. 6, fig. 75 (late Eocene, southern England).

*Terebellum convolutum* Lamarck, 1802, Ann. Mus. National Hist. Nat., vol. 1, p. 390; Lamarck, 1805, Ann. Mus. Hist. Nat. Paris, vol. 6, p. 225, pl. 44, figs. 3a, 3b; Lamarck, 1811, Ann. Mus. Hist. Nat. Paris, vol. 16, p. 302; Lamarck, 1822, Histoire naturelle des animaux sans vertèbres, vol. 7, p. 411; Blainville, 1825-1827, Manuel de malacologie et de conchyliologie, p. 416, 1825, Atlas, pl. 27, figs. 2, 2a, 1827; Deshayes, 1824-1837, Description des coquilles fossiles des environs de Paris, vol. 2, p. 737, 1837, Atlas, pl. 95, figs. 32, 33; Bronn, 1838, Lethaea geognostica, vol. 2, p. 1113, Atlas, pl. 42, figs. 13a, 13b, 1837; d'Archiac, *in* Tchihatcheff, 1850, Bull. Soc. géol. France, sér. 2, vol. 7, p. 405

(Eocene, Asia Minor); Quenstedt, 1852, Handbuch der Petrefaktenkunde, p. 439, pl. 35, fig. 4; Cailliaud, 1856, Bull. Soc. géol. France, sér. 2, vol. 13, pp. 41, 42 (middle Eocene, northwestern France); de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi. Palermo; p. 23, pl. 1, fig. 20 (Lutetian, northern Italy); Vasseur, 1881, Recherches géologiques sur les terrains tertiaires de la France occidentale. Stratigraphie. Première partie: Bretagne. Paris; p. 232 (middle Eocene, northwestern France); de Gregorio, 1894, Ann. Géol. Paléont., Livraison 14, p. 11, pl. 1, figs. 14-20 (early Eocene, northern Italy); Koch, 1894, Mitt. Jb. königl. ungar. geol. Anstalt, vol. 10, pp. 277, 285 (middle Eocene, Rumania).

*Terebellum convolutum* ? Lamarck, Bellardi, 1852, Mém. Soc. géol. France, ser. 2, vol. 4, pt. 2, pp. 217, 291 (late middle Eocene, southeastern France).

*Terebellum convolutum* (Lamarck), Perreau, 1968, Mém. Bureau Rech. Géol. Min., No. 58, p. 212 ("middle Bartonian" of Quoniam, northwest of Paris, France).

*Terebellum (Seraphs) convolutum* Lamarck, Cossmann, 1904, Essais de paléoconchologie comparée, sixième livraison, p. 45, pl. 1, fig. 1 (Lutetian of Paris Basin); Malaroda, 1954, Mem. Ist. Geol. Min. Univ. Padova, vol. 19, pp. 57, 82 (part), pl. 4, figs. 3-5, pl. 12, figs. 13, 21 (early Eocene of Monte Postale, northern Italy).

*Seraphs convolutus* Lamarck, Montfort, 1810, Conchyliologie systématique, vol. 2, pp. 374 (fig.), 375; J. Sowerby, 1821, The Mineral Conchology of Great Britain, vol. 3, p. 155, pl. 286.

*Terebellum* cf. *convolutum* Lamarck, Schlosser, 1925, Abh. Bayer. Akad. Wiss., math.-naturwiss. Abt., vol. 30, No. 7, pp. 34, 47, pl. 8, fig. 14 ("upper Eocene", Bavaria).

*Terebellum convolutum roncanum* de Gregorio, 1896, Ann. Géol. Paléont., livraison 21, p. 35, pl. 3, fig. 4 (late middle Eocene of Roncá, northern Italy).

*Terebellum subbelemnitoideum* d'Archiac and Haime, 1854, Description des animaux fossiles du groupe nummulitique de l'Inde, seconde livraison, p. 333, pl. 32, figs. 16, 16a; Cox, 1931, Trans. Roy. Soc. Edinburgh, vol. 57, No. 2, p. 52 [Laki beds (early Eocene), India].

*Terebellum subbelemnitoideum* d'Archiac, Mayer, 1866, Vierteljahrsschrift Naturf. Ges. Zürich, Jg. 11, pp. 319, 332 (Lutetian of Armenia; Bartonian of Switzerland).

*Terebellum obtusum* J. de C. Sowerby, d'Archiac and Haime, 1854, Description des animaux fossiles du groupe nummulitique de l'Inde, seconde livraison, p. 333, pl. 32, fig. 20 (not fig. 21) [Laki beds (early Eocene), India]; Doncieux, 1905, Ann. Univ. Lyon, n.s., I. Sci., Méd., fasc. 17, p. 44, pl. 2, fig. 4 (late Paleocene, southern France).

*Terebellum* cf. *obtusum* J. de C. Sowerby, Cuvillier, 1933, Mém. Inst. Egypte, vol. 22, p. 45, pl. 5, figs. 21, 23 ["upper Lutetian (middle Eocene)", Egypt].

*Terebellum carcassense* Leymerie, 1846, Mém. Soc. géol. France, sér. 2, vol. 1, pt. 2, pp. 353, 365, 371, pl. 16, figs. 9a, 9b ("au nord de Carcassonne, dans le calcaire à nummulites de la Montagne Noire." Late Paleocene, southern France); d'Orbigny, 1850-1852, Prodrome de paléontologie . . ., vol. 2, p. 314, 1850; Mallada, 1890, Bol. Comisión Mapa Geol. España, vol. 16, p. 117 (Eocene, northern Spain); Mallada, 1892, Bol. Comisión Mapa Geol. España, vol. 18, p. 206 (Eocene, Spain); Vinassa de Regny, 1896, Palaeont. Italica, vol. 1, pp. 230, 259; de Gregorio, 1896, Ann. Géol. Paléont., livraison 21, p. 36; Doncieux, 1905, Ann. Univ. Lyon, n.s., I. Sci., Méd., fasc. 17, p. 45, pl. 2, fig. 2 (late Paleocene, southern France); Doncieux, 1908, Ann. Univ. Lyon, n.s., I. Sci., Méd., fasc. 22, p. 91 (late Paleocene, southern France); Fabiani, 1915, Mem. Ist. Geol. Univ. Padova, vol. 3, Mem. 1, pp. 255, 261 (middle Eocene, northern Italy); Schlosser, 1925, Abh. Bayer. Akad. Wiss., math.-naturwiss. Abt., vol. 30, No. 7, p. 161; Cox, 1931, Trans. Roy. Soc. Edinburgh, vol. 57, No. 2, p. 51, pl. 1, fig. 21 (Laki of Sind and Salt Range; Khirthar of Sind: early and middle Eocene); Cox, 1936, Palaeont. Indica, n.s., vol. 22, Mem. 2, p. 28, pl. 3, figs. 7-9 (middle Eocene of Bahrein Island, Persian Gulf); Furon, 1941, Mém. Mus. National Hist. Nat., n.s., vol. 7, fasc. 2, p. 335 (Lutetian of Bahrein Island, Persian Gulf); Eames, 1952, Philos. Trans. Roy. Soc. London, ser. B, No. 631, vol. 236, p. 73 (lower, middle, and upper Eocene, Pakistan and northwestern India). For additional citations see this publication.

*Terebellum carcassonense* Leymerie, Mayer, 1866, Vierteljahrsschrift Naturf. Ges. Zürich, Jg. 11, pp. 319, 332 (Bartonian of Switzerland).

*Terebellum carcassonnense* Leymerie, Bellardi, 1852, Mém. Soc. géol. France, sér. 2, vol. 4, pt. 2, pp. 217, 291 (late middle Eocene, southeastern France); Vinassa de Regny, 1898, Palaeont. Italica, vol. 3, pp. 147, 158, 164 (Eocene, northern Italy).

*Terebellum (Terebellum) carcassense* Leymerie, Bagmanov, 1966, Larger Foraminifera and mollusk fauna of the Eocene deposits of the Trans-Caucasus (in Russian), Baku, p. 179, pl. 81, figs. 5, 6 (middle Eocene, Trans-Caucasus).

*Terebellum* cf. *carcasense (sic)* Leymerie, Schlosser, 1925, Abh. Bayer. Akad. Wiss., math.-naturwiss. Abt., vol. 30, No. 7, pp. 103, 179, pl. 2 (not pl. 3 as indicated), fig. 27 (Lutetian, Bavaria).

*Terebellum* cf. *carcassense* Leymerie, Cuvillier, 1933, Mém. Inst. Egypte, vol. 22, p. 45, pl. 4, figs. 21, 22 (upper Lutetian, Egypt).

*Terebellum belemnitoideum* d'Archiac, *in* Tchihatcheff, 1850, Bull. Soc. géol. France, sér. 2, vol. 7, p. 405 (*nomen nudum*) (Eocene, Asia Minor); Koch, 1894, Mitt. Jb. königl. ungar. geol. Anstalt, vol. 10, pp. 277, 285 (Eocene, Rumania).

? *Terebellum perconvolutum* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi, Palermo, p. 23, (Lutetian, northern Italy).

? *Terebellum retractum* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi, Palermo, p. 22, pl. 5, figs. 24, 25 (Lutetian, northern Italy).

? *Terebellum saldatum* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi, Palermo, p. 22, pl. 5, fig. 22 (Lutetian, northern Italy).

? *Terebellum postturgidum* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi. Palermo, p. 23, pl. 5, fig. 33 (Lutetian, northern Italy).

? *Terebellum superbum* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi, Palermo, p. 23, pl. 1, fig. 19 (Lutetian, northern Italy).

? *Terebellum* cf. *belemnitoideum* d'Archiac, Pavay, 1873, Mitt. Jb. königl. ungar. geol. Anstalt, vol. 1, pt. 3, p. 412 (Eocene, Rumania).

? *Terebellum clava* Schafhäutl, 1863, Süd-Bayerns Lethaea Geognostica. Leipzig; p. 209, Atlas, pl. 47, fig. 14 (Lutetian, Bavaria).

? *Terebellum oliviforme* Mayer, 1866, Vierteljahrsschrift Naturf. Ges. Zürich, Jg. 11, pp. 319, 332 (Bartonian of Akhaltsikhe near Tiflis, Georgia, USSR; not Tongrian: see discussion below).

? *Terebellum lanceolatum* de Gregorio, 1880 (not Cossmann and Pissarro, 1909), Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi, Palermo, p. 23, pl. 5, fig. 28 (Lutetian, northern Italy).

? *Terebellum obvolutum* Brongniart, 1823, Mémoire sur les terrains de sédiment supérieurs calcaréo-trappéens du Vicentin. Paris, p. 62, pl. 2, figs. 15a, 15b (late middle Eocene of Roncá, northern Italy); d'Orbigny, 1850-1852, Prodrome de paléontologie . . . , vol. 2, p. 314, 1850; Doncieux, 1905, Ann. Univ. Lyon, n.s., I. Sci., Méd., fasc. 17, p. 44, pl. 2, fig. 3; Fabiani, 1915, Mem. Ist. Geol. Univ. Padova, vol. 3, Mem. 1, p. 143 (middle Eocene, northern Italy).

? *Terebellum plicatum* d'Archiac and Haime, 1854, Description des animaux fossiles du groupe nummulitique de l'Inde; seconde livraison, p. 334, pl. 32, fig. 22 (not figs. 17, 18).

Not *Terebellum convolutum* Lamarck, Grateloup, 1833, Actes Soc. Linn. Bordeaux, vol. 6, p. 314 (Oligocene, southwestern France) [= *Seraphs subconvolutus* (d'Orbigny)]; Grateloup, 1840-1846, Conchyliologie fossile des terrains tertiaires du bassin de l'Adour (environs de Dax), pl. 42, fig. 1 (Oligocene, southwestern France) [= *Seraphs subconvolutus* (d'Orbigny)].

*Terebellum fusiformopse* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi. Palermo, p. 22, pl. 5, fig. 29 (Lutetian, northern Italy); Oppenheim, 1896, Palaeontographica, vol. 43, p. 194 (early Eocene of Monte Postale, northern Italy); Oppenheim, 1896, Zs. deutschen geol.

Ges., vol. 48, p. 72; Oppenheim, 1906, Palaeontographica, vol. 30, 3. Abt., 2. Lief., p. 299 (middle Eocene, Egypt); Fabiani, 1915, Mem. Ist. Geol. Univ. Padova, vol. 3, pp. 255, 261 (middle and upper Eocene, northern Italy); Cuvillier, 1930, Mém. Inst. Egypte, vol. 16, p. 253 (middle (?) Eocene, Egypt); Eames, 1952, Philos. Trans. Roy. Soc. London, ser. B, No. 631, vol. 236, p. 74, pl. 3, figs. 76a, b (middle Eocene, Pakistan).

*Terebellum (Seraphs) fusiformopse* de Gregorio, Malaroda, 1954, Mem. Ist. Geol. Min. Univ. Padova, vol. 19, p. 58 (early Eocene of Monte Postale, northern Italy).

Not *Terebellum fusiformopse* de Gregorio, Cossmann, 1889, Ann. Soc. Roy. Malac. Belgique, vol. 24, p. 97, pl. 3, figs. 3, 4 (= *Seraphs leukoleptus*, n. sp.). Cossmann and Pissarro, 1906-1913, Iconographie complète des coquilles fossiles de l'éocène des environs de Paris, vol. 2, pl. 31, fig. 158-3, 1911 (= *Seraphs leukoleptus*, n. sp.).

*Terebellum obesum* Mayer, 1866, Vierteljahrsschrift Naturf. Ges. Zürich, Jg. 11, pp. 320, 333 [middle (?) Eocene, Armenia].

*Terebellum (Seraphs ?)* cf. *sopitum* Solander var., Meffert, 1931, Trans. Geol. Prospecting Service USSR, fasc. 99, pp. 43, 58, pl. 8, figs. 6, 7 ("middle Eocene", Armenia).

*Terebellum (Seraphs) sopitum* Solander, var. ?, Isaeva, 1933, Trans. United Geol. Prosp. Service USSR, fasc. 305, p. 32, pl. 3, fig. 12 (Eocene of Georgia, USSR).

*Terebellum (Seraphs) sopitum* Solander var. *giganticum* Korobkov, Mészáros, 1957, Mon. Geol. Paleont. (Ed. Acad. Rep. Pop. Rumania), No. 1, p. 145, pl. 28, figs. 5, 5a, pl. 29, figs. 2, 2a, 2b (upper Eocene of Cluj basin, Rumania).

*Terebellum (Seraphs) sopitum* Solander var. *gigantica* (*sic*) Korobkov, Gabrielian, 1964, Paleogene and Neogene of the Armenian SSR (in Russian). Yerevan, p. 78 (upper Eocene, Armenia).

*Terebellum (Seraphs) sopitum* Solander var. *daralagiosicum* n. var. in lit., Gabrielian, 1964, Paleogene and Neogene of the Armenian SSR (in Russia). Yerevan, p. 78 (upper Eocene, Armenia).

*Terebellum (Seraphs) korobkowi* Bagmanov, 1966, Larger Foraminifera and mollusk fauna of the Eocene deposits of the Trans-Caucasus (in Russian). Baku, p. 181, pl. 85, fig. 1 (middle Eocene, Trans-Caucasus).

*Terebellum (Seraphs) issaevae* Bagmanov, 1966, *ibidem*, p. 181, pl. 83, figs. 2-5 (middle and upper Eocene, Trans-Caucasus).

*Terebellum (Terebellum) paradaschensis* Bagmanov, 1966, *ibidem*, p. 181, pl. 84, figs. 1-4 (middle Eocene, Trans-Caucasus).

*Terebellum fusiforme* Lamarck, J. Sowerby, 1821, The Mineral Conchology of Great Britain, vol. 3, p. 157 (part), pl. 287 (upper figures only) (upper Eocene, southern England); Favre, 1918, Catalogue illustré de la collection Lamarck. Mollusques trachélipodes fossiles. Geneva; pl. 13, figs. 209a-b.

*Description.* — Of medium to large size. Shell slightly inflated during immature stages but more so in adult stage. Height of spire variable. Apex blunt to somewhat pointed. Surface smooth except for undulating growth lines. Outer lip not thickened. Callus of inner lip thin. Columella slightly bent backwards near base.

*Lectotype (herewith selected).* — British Museum (Natural History), Dept. of Palaeontology, No. GG 21010.

*Dimensions of lectotype.* — Height 26.4 mm.

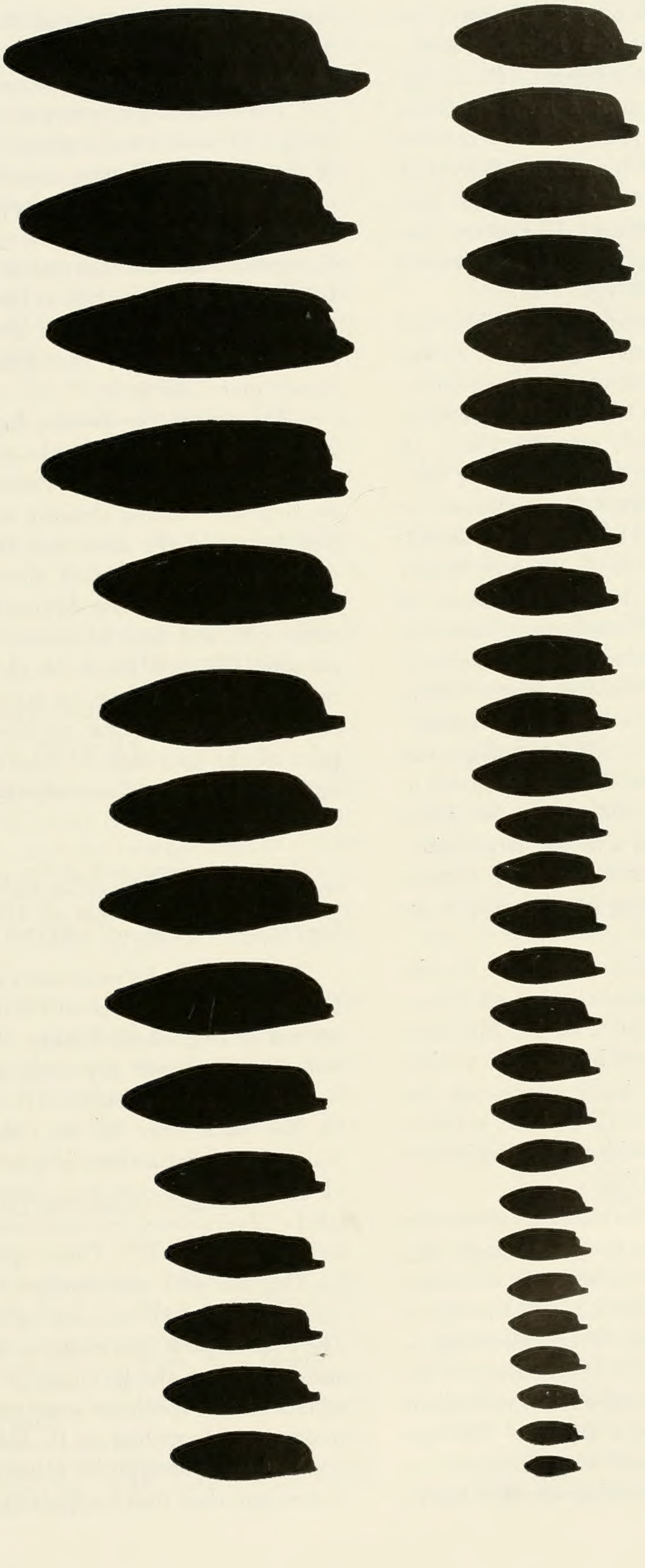
*Type locality.* — "Cliffs by the village of Hordwell, which is nearly midway between Christ Church and Lymington, Hampshire County. Found below a stratum of gravel and sand, about 14 or 15 feet thick, in a bluish kind of clay or marl, quite down to the level of the sea". Bartonian (late Eocene).

The lectotype of *S. sopitus* (see Pl. 1, figs. 1-3) is a slender, immature shell. The original figure shows a specimen, of which part of the shell of the body whorl is broken away. Since Solander's time the specimen has been damaged still more. The diameter of the lectotype is, therefore, not given above. Besides the lectotype there is one paralectotype in the Brander collection of the British Museum (No. GG 21011) which remains unfigured. The type specimen of *Bulla volutata* Solander (1766, p. 34, pl. 6, fig. 75) was collected at the same locality as the lectotype of *S. sopitus*. It represents an adult shell of *S. sopitus* (height about 60 mm) with a fairly pointed spire.

*S. sopitus* as here interpreted shows a remarkable variability. Disagreements about the interpretation of *S. sopitus* started with the introduction of the name *convolutus* by Lamarck (1802, p. 390) for specimens of *S. sopitus* from the Lutetian of the Paris Basin (Grignon is the type locality of *convolutus*) and still go on in recent literature (*e.g.* Bagmanov, 1966, pp. 180-181). It should be pointed out that discussions of that sort should be based on well-preserved material, *i.e.* on specimens with their actual shell. The occurrences of shelled specimens, however, are practically restricted to the Bartonian of southern England and the Lutetian of the Paris Basin. Specimens from most other localities are preserved as internal casts, and in many cases they are deformed.

At certain localities *S. sopitus* occurs in large numbers (up to 100 specimens) according to the material at hand: at several localities in the Paris Basin (*e.g.* Grignon, Villiers-St-Frédéric), in northern Italy (*e.g.* San Giovanni Ilarione), in Rumania (*e.g.* Monoster, Cluj Basin), and in Egypt (*e.g.* Mount Mokattam near Cairo). This observation has been made by Pavay (1873, p. 363) and Cuvillier (1930, p. 179). Most of the perfectly preserved shells from the middle Eocene of Villiers-Saint-Frédéric near Paris show remnants of the color pattern which consists of many small, somewhat irregular dots.

As pointed out in the description of *S. sopitus* this species is variable as to height of spire, acuteness of spire and inflation of body whorl (see also Text-figure 14). Specimens from the Bartonian of southern England are somewhat stouter than material from the Lutetian of the Paris Basin and their spire is blunter and shorter on an average. The Lutetian beds at Chaussy (Seine-et-Oise, France) have yielded specimens of *S. sopitus* of extraordinary size (see Pl. 2, figs. 5-7). These large shells have a higher spire and are more slender than English ones, but smaller specimens from Chaussy are practically indistinguishable from their English counterparts. Perfectly pre-



Text-figure 14. *Seraphs sopitus* (Solander). Natural size. All specimens from the Lutetian of Grignon near Paris. Series of shells showing gradual change of shape during ontogeny.

served shells of similar size occur not only at Chaussy, but also at Grignon (collection at Ecole des Mines, Paris).

The large shell from Chaussy here figured (Pl. 2, figs. 5-7) reaches a height of almost 80 mm; a large specimen from Barton (Pl. 1, figs. 18-19) 65 mm, and another one from the late middle Eocene of Roncá, northern Italy (Pl. 3, fig. 9) more than 80 mm. Even higher specimens are here figured from the middle Eocene of Mount Mokattam near Cairo (Pl. 2, figs. 3-4), and from the upper (?) Eocene of Monoster, Cluj Basin, Rumania (Pl. 2, figs. 1-2).

The occurrences of large specimens in the middle and upper Eocene of some eastern countries gave rise to discussions and the introduction of new names for these forms by Meffert (1931, pp. 43, 58) Isaeva (1933, p. 32), Mészáros (1957, p. 145), and Bagmanov (1966, pp. 180, 181). All these authors overlooked that Mayer (1866, pp. 320, 333) had already introduced the name *Terebellum obesum* for large specimens from the middle (?) Eocene of Djulfa, Armenia. In the original description of *T. obesum* Mayer listed the collection number Du 192 for the specimens he had at hand. In the collection of Mayer-Eymar, however, there are no specimens with this number. Instead three internal casts were found with the following label: "*Terebellum obesum,* Djoulfa (Arménie), Parisien I ?, Original". The largest of these three specimens is 108.4 mm high and 42 mm wide, and thus agrees with the dimensions given in the original description. Using this indication the three specimens are considered as syntypes, and the large specimen is, therefore, selected as the lectotype of *T. obesum* (see Pl. 4, figs. 1-2). The two remaining paralectotypes are also figured (Pl. 4, figs. 3-4).

According to written communication from I. A. Korobkov the combination *Terebellum (Seraphs) sopitum* Solander var. *giganticus* (*sic*) var. nova as cited by Mészáros (1957, p. 145) has never been published by Korobkov himself, but by other authors. Korobkov is, therefore, not the author of the name *giganticus* as stated by those authors, and the introduction of the name *korobkowi* by Bagmanov (1966, p. 181) for this form is unjustified.

In the original description of *Terebellum oliviforme* Mayer (1866, p. 332) referred to three specimens under the collection number Du 193. The type locality is indicated as Akhaltsikhe near Tiflis (Georgia, USSR), and the age is given as Tongrian. However, only one of the three specimens could be found in the collection of Mayer-Eymar. Its measurements do not agree with those given in the original description, but it certainly represents a syntype. The age on the original label has been changed from Tongrian to Bartonian I by Mayer. This only available syntype represents an incompletely preserved internal cast (Pl. 4, fig. 5), and was possibly a moderately sized *S. sopitus. Terebellum oliviforme* should be considered as a *nomen dubium.*

*Terebellum fusiformopse* de Gregorio (1880, p. 22, pl. 5, fig. 29), which was originally described from the Lutetian of San Giovanni Ilarione, northern Italy, is considered as a synonym of *S. sopitus.* The type is a small (height 37 mm) specimen and is not more slender than immature shells of *S. sopitus* from the Bartonian of southern England or the Lutetian of the Paris Basin. De Gregorio (1880, p. 23) commented upon the quality of his original figure pointing out, among other things, that the sutures should have been drawn more obliquely.

*Terebellum carcassense* Leymerie (1846, pp. 353, 365, 371, pl. 16, figs. 9a, 9b) was originally described from beds now referred to the late Paleocene. The original figure is an idealised drawing showing a specimen with a moderately high spire. All the specimens from the type area of *T. carcassense* (south slope of the Montagne Noire, north of Carcassonne, southern France) are preserved as internal casts only, and their identification, therefore, remains questionable. Cox (1931b, p. 51, pl. 1, fig. 21) separated *T. carcassense* from *S. sopitus* on account of its lower spire, but he stated that both forms are closely related. The top of the spire of the specimen he figured (here refigured on Pl. 4, figs. 10-11) is not preserved which gives the impression of a low spire.

Another specimen with a low spire from the early Eocene Laki beds of Sind has been described and figured by Cox (1931b, p. 52, pl. 1, fig. 16) under the name of *Terebellum* sp. It is identified as *Seraphs (Seraphs)* sp. and refigured here on Pl. 5, figures 1, 2.

*Terebellum belemnitoideum* d'Archiac was listed by Tchihatcheff (1850, p. 405) from an unspecified Eocene horizon at Zafranboli, Turkey. The name of this species was introduced without any description and no specimen was figured. *T. belemnitoideum* is, therefore, a *nomen nudum.* In the collections of the Muséum National d'Histoire Naturelle in Paris there is a lot (No. B 22388) containing 11 more or less incomplete, internal casts with the following label: "*Terebellum belemnitoideum* d'Archiac. Tertiaire inférieur. Zafiranboli". These specimens had been collected by Tchihatcheff, who handed them over to d'Archiac for study. They obviously represent syntypes of this species. The best of these specimens is here figured (Pl. 3, figs. 6-8) and selected as the lectotype of *T. belemnitoideum.* On the surface of this specimen some sections of nummulites can be recognized. According to H. Schaub (personal communication) these nummulites cannot be identified with confidence, but they make a Lutetian age highly probable.

The list of synonyms of S. *sopitus* contains a number of questionable entries. Most of these "species" were based on unsatisfactory material and should be considered as *nomina dubia*. The list of synonyms is not as critical as it should be. Many entries are taken from faunal lists only, and in many cases there is no stratigraphic control. For this reason some of the age indications have been put in quotation marks.

*Distribution.* — Late Paleocene: France. Eocene: Spain, Yugoslavia, Rumania, Turkey, Georgia (USSR), Persia, Madagaskar (collection of the Muséum National d'Histoire Naturelle Paris, No. B 23194).

Lower Eocene: Egypt, Pakistan, India.

Middle Eocene: France, Spain, Belgium, Germany, Italy, Yugoslavia, Rumania, Turkey, Egypt, Nakhichevan ASSR (USSR), Armenia, Crimea (?), Bahrein Island (Persian Gulf), Pakistan, India.

Upper Eocene: England, France, Belgium, Germany, Switzerland, Italy, Rumania, Egypt, Georgia (USSR), Crimea (?), Pakistan, India.

Oligocene: England (record based on Newton, 1891, p. 98). This record is doubtful and needs confirmation.

### **Seraphs (Seraphs) cf. sopitus** (Solander)

Plate 5, figures 3-4

A single specimen of a species of *Seraphs* (height 50.6 mm; maximum diameter 18.5 mm) from an old collection in the U.S. National Museum with the number USNM 135098 has the following label: "near Port Antonio, Jamaica. Presumably White Limestone". The specimen is an incomplete, internal cast, and it is not possible to give a definite identification.

Although the Seraphsidae are well represented in the Paleogene of Jamaica, the occurrence of this specimen is noteworthy, because it is the only one belonging to the genus *Seraphs s. str.* The White Limestone near Port Antonio, from which it is said to have been collected is of middle or more probably late Eocene age.

### **Seraphs (Seraphs) olivaceus** (Cossmann)

Plate 5, figures 5-11, Text-figure 15

*Terebellum (Seraphs) olivaceum* Cossmann, 1889, Ann. Soc. Roy. Malac. Belgique, vol. 24, p. 97, pl. 3, figs. 1, 2 (middle Eocene, Paris Basin); Cossmann and Pissarro, 1906-1913, Iconographie complète des coquilles fossiles de l'éocène des environs de Paris, vol. 2, pl. 31, fig. 158-4, 1911 (middle Eocene, Paris Basin).

? *Terebellum cf. olivaceum* Cossmann, Oppenheim, 1894, Zeitschrift deutschen geol. Ges., vol. 46, pp. 411, 438, pl. 26, figs. 14a, 14b (middle Eocene, northern Italy).

? *Terebellum (Seraphs) fusiforme* Lamarck, Tessier, 1952, Contributions à la stratigraphie et à la paléontologie de la partie ouest du Sénégal (Crétacé et Tertiaire). Dakar, tome 2, p. 374, pl. 32, figs. 16-18 (middle Eocene, Senegal).

*Description.* — Of medium size, moderately slender. Spire acute, its sides straight. Line of greatest diameter of shell lies just below the adapical end of the aperture. Surface smooth except for faint, somewhat sinuous growth lines. Callus of inner lip thin, inconspicuous, broken away in most specimens. Outer lip not thickened, sinuous when viewed in profile. Columella slightly bent backwards near base. Base of outer lip does not reach down to the level of the base of the columella.

*Type.* — Cossmann's figure represents a specimen from the Lutetian of Chaussy collected by Bernay. This specimen is the holotype, but it has not been found in the collections of the Ecole des Mines de Paris, Laboratoire de Paléontologie.

*Dimensions of holotype.* — The dimensions are given by Cossmann as: height 32 mm; maximum diameter 9 mm. The figured specimen, the holotype, is said to be reproduced in natural size. The measurements taken from that figure, however, are: height 29.2 mm; maximum diameter 8.0 mm.

*Type locality.* — Chaussy, Dept. Seine-et-Oise, France. Lutetian (middle Eocene).

So far S. *olivaceus* has been found at the following localities in the Lutetian of the Paris Basin: Chaussy, Vaudancourt, Parnes.

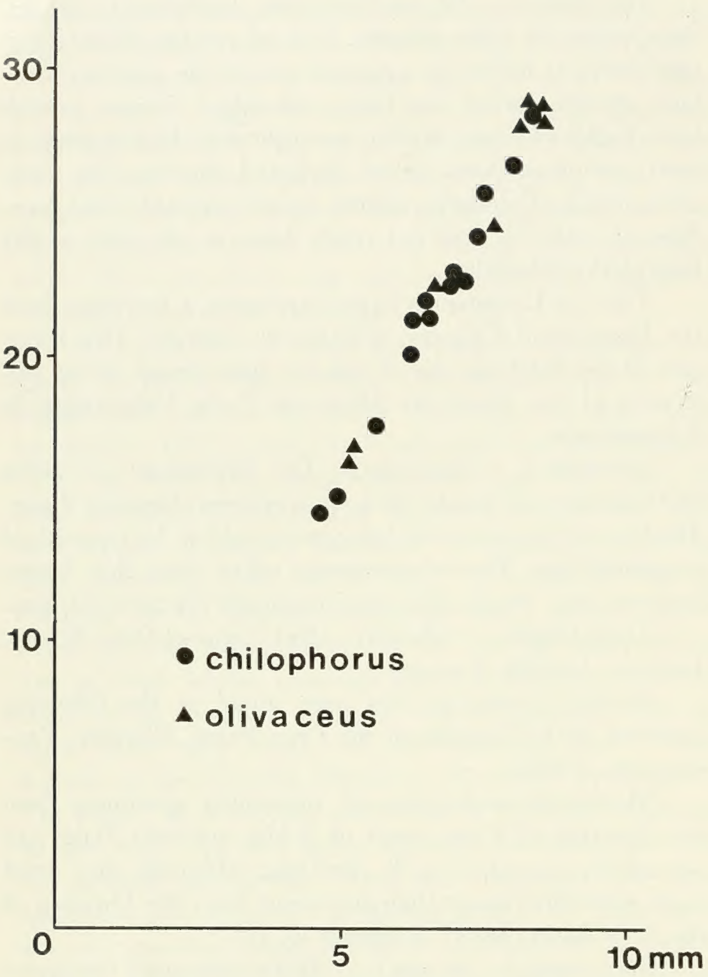
Moderately well-preserved, incomplete specimens from the Lutetian of Piana, west of Schio, northern Italy, are tentatively identified as S. *olivaceus*, although they tend to be somewhat larger than specimens from the Lutetian of the Paris Basin (see Pl. 5, figures 10, 11).

*Measurements (in mm).* — All the measured specimens are from Chaussy, the type locality.

| height | diameter | ratio |
|---|---|---|
| 16.4 | 5.1 | 3.2 |
| 16.9 | 5.2 | 3.3 |
| 22.4 | 6.7 | 3.3 |
| 24.4 | 7.6 | 3.2 |
| 28.2 | 8.2 | 3.4 |
| 28.4 | 8.5 | 3.3 |
| 28.7 | 8.4 | 3.4 |
| 28.9 | 8.3 | 3.5 |

S. *olivaceus* is much smaller than S. *sopitus*, and its apex is more pointed. Immature shells of S. *sopitus* still have a less pointed apex. Although S. *olivaceus* and S. *chilophorus* have similar dimensions and proportions, they can clearly be distinguished. These differences are pointed out under S. *chilophorus*.

*Distribution.* — Middle Eocene, Paris Basin, France, northern Italy (?), Senegal (?).



Text-figure 15. Graph showing the height/diameter relationships of *S. chilophorus* and *S. olivaceus.*

### **Seraphs (Seraphs) chilophorus** (Cossmann)

Plate 5, figures 12-21; Text-figures 15, 16

*Terebellum (Seraphs) chilophorum* Cossmann, 1889, Ann. Soc. Roy. Malac. Belgique, vol. 24, p. 98, pl. 3, figs. 5, 6 (middle Eocene, Paris Basin); Cossmann, 1904, Essais de paléoconchologie comparée, livraison 6, p. 45, pl. 2, fig. 6 (middle Eocene, Paris Basin); Cossmann and Pissarro, 1906-1913, Iconographie complète des coquilles fossiles de l'éocène des environs de Paris, vol. 2, pl. 32, fig. 158-5, 1911 (middle Eocene, Paris Basin).

*Description.* — Shell of medium size, moderately slender. Surface sculptured by inconspicuous growth lines and narrow axial grooves which are parallel to the growth lines. These grooves are somewhat oblique on the upper half of the spire, turn to an axial direction below until they run to the right terminating at the edge of the inner lip. Callus of inner lip well developed and well separated from surface of shell. Columella bent backwards near base. Outer lip slightly thickened, not reaching as far down as the columella. Outer lip slightly sinuous near the adapical end of the aperture. The continuation of the outer lip on the spire is somewhat more thickened than below. It extends to the apex and continues on the opposite side of the apex for a short distance as an "apical canal". The callus of the inner lip has a continuation on the spire as well forming a narrow band parallel to the continuation of the outer lip.

*Type.* — Cossmann's original figure represents a specimen from the Lutetian of Chaussy collected by Bernay. This specimen is the holotype, but it has not been found in the collections of the Ecole des Mines de Paris, Laboratoire de Paléontologie.

*Dimensions of holotype.* — Height 29 mm; maximum diameter 8 mm.

*Type locality.* — Chaussy, Dept. Seine-et-Oise, France. Lutetian (middle Eocene).

So far *S. chilophorus* has been found at the following localities in the Lutetian of the Paris Basin: Chaussy, Saulx-Marchais, Parnes, Grignon, Les Boves.

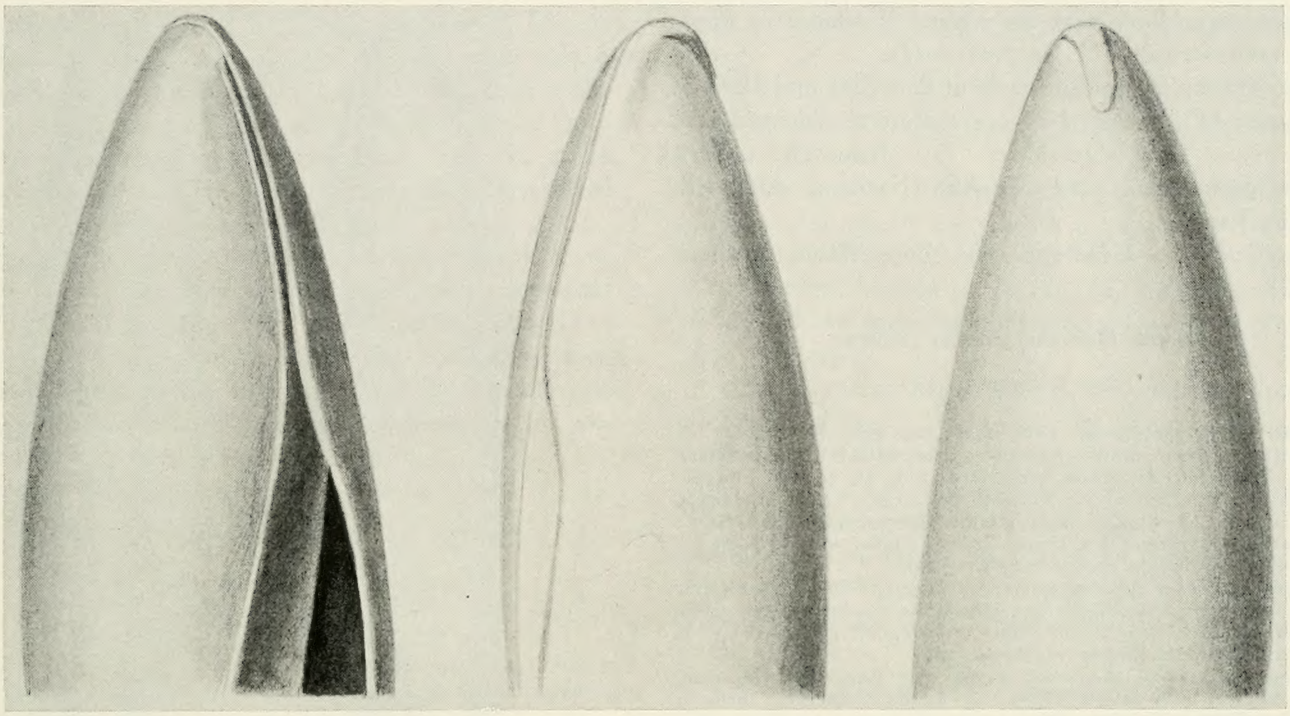
*S. chilophorus* shows typical features of the genus *Seraphs*: the largest diameter of the shell is situated at a level near the adapical end of the aperture and the outer lip is characteristically sinuated. The tendency to develop a short "apical canal", on the other hand, is reminiscent of the posterior canal of *Paraseraphs* (see Text-figure 16).

*Measurements (in mm).* — All the measured specimens are from Chaussy, the type locality.

| height | diameter | ratio |
|---|---|---|
| 14.4 | 4.6 | 3.1 |
| 15.1 | 4.9 | 3.1 |
| 17.6 | 5.6 | 3.1 |
| 20.1 | 6.2 | 3.2 |
| 21.2 | 6.3 | 3.4 |
| 21.3 | 6.5 | 3.3 |
| 22.0 | 6.5 | 3.4 |
| 22.5 | 6.9 | 3.3 |
| 22.7 | 7.1 | 3.2 |
| 22.8 | 7.0 | 3.3 |
| 24.2 | 7.4 | 3.3 |
| 25.7 | 7.5 | 3.4 |
| 26.6 | 8.0 | 3.3 |
| 28.5 | 8.3 | 3.4 |

*S. chilophorus* is closely related to *S. olivaceus,* with which it occurs together in the Lutetian of Chaussy. *S. olivaceus* is higher on an average, lacks the sculpture of *S. chilophorus,* has a more pointed spire, and does not develop a short "apical canal". In addition the base of the columella is much more bent backwards in *S. chilophorus.* The "posterior canal" of *S. chilophorus* is similar to that of *S. mayeri* (see under that species).

*Distribution.* — Middle Eocene, Paris Basin (France).



Text-figure 16. Three views of posterior portion of shell of *Seraphs chilophorus* showing "apical canal". Lutetian of Chaussy. Ecole des Mines de Paris, Laboratoire de Paléontologie, unnumbered. Coll. Deshayes. Sculpture omitted; 6 ×.

### **Seraphs (Seraphs) leukoleptus**, n. sp.

Plate 6, figures 1-3, Text-figure 17

*Terebellum fusiformopse* de Gregorio, Cossmann, 1889, Ann. Soc. Roy. Malac. Belgique, vol. 24, p. 97, pl. 3, figs. 3, 4 (middle Eocene, Paris Basin); Cossmann and Pissarro, 1906-1913, Iconographie complète des coquilles fossiles de l'éocène des environs de Paris, vol. 2, pl. 31, fig. 158-3, 1911 (middle Eocene, Paris Basin).

? *Terebellum pectinatum* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi. Palermo, p. 22, pl. 1, fig. 17 (*nomen dubium*) (middle Eocene, northern Italy).

*Description.* — Of medium size, slender. Shell becomes gradually broader toward the base. Surface smooth except for inconspicuous growth lines and a few faint spiral grooves near the base. Columella but slightly bent backwards near base. Callus of inner lip conspicuous, well separated from surface of shell, and reaching up to the apex. Outer lip almost straight when viewed in profile, slightly thickened, somewhat opisthocline. Basal margin of body whorl situated only a little above the base of the columella.

*Holotype.* — Ecole des Mines de Paris, Laboratoire de Paléontologie, unnumbered.

*Dimensions of holotype.* — Height 27.6 mm; maximum diameter 6.2 mm.

*Type locality.* — Chaussy, Dept. Seine-et-Oise, France. Lutetian (middle Eocene).

So far this species is only known from the type locality with certainty. It is based on six almost perfectly preserved specimens which are deposited at the Ecole des Mines de Paris, Laboratoire de Paléontologie. The holotype was collected by Deshayes. On the last part of its body whorl an interruption in growth is marked conspicuously by a former outer lip.

As mentioned under *Paraseraphs propedistortus*, *S. leukoleptus* appears to represent a stage intermediate between *Seraphs* and *Paraseraphs*: it has the slender, fusiform shape of species of *Paraseraphs* but is entirely involute like species of *Seraphs*.

*S. leukoleptus* is distinguished from all the other species of *Seraphs* by its slender, fusiform shape. This shape recalls *Terebellum pectinatum* de Gregorio (1880, p. 22, pl. 1, fig. 17) from the Lutetian of San Giovanni Ilarione, northern Italy, which, however, seems to attain a larger size, and which is said to be sculptured by some spiral lines near the apex. *T. pectinatum* was based on unsatisfactory material preserved as internal casts and is here considered as a *nomen dubium*. Among the rich material from San Giovanni Ilarione, the type locality of *T. pectinatum*, at hand no specimens approach *T. pectinatum*. Although *T. pectinatum* is tentatively put in the synonymy of *S. leukoleptus*, better topotypes might show that the species is related to *Paraseraphs armoricensis* or *P. propedistortus*.

Two incomplete specimens from San Giovanni Ilarione here figured (Pl. 6, figs. 4-8) are tentatively identified as *S. leukoleptus*. They were collected by Meneguzzo in 1872 and are deposted at the Muséum National d'Histoire Naturelle, Paris.

*Distribution.* — Middle Eocene, Paris Basin, northern Italy (?).

### **Seraphs (Seraphs) plicifer** (Bayan)

Plate 7, figures 1-17

*Terebellum pliciferum* Bayan, 1870, Bull. Soc. géol. France, sér. 2, vol. 27, p. 481 (middle Eocene, northern Italy); Oppenheim, 1894, Zeitschrift deutschen geol. Ges., vol. 46, p. 438 (middle Eocene, northern Italy); Vinassa de Regny, 1896, Palaeont. Italica, vol. 1, pp. 230, 260 (middle Eocene, northern Italy); Fabiani, 1915, Mem. Ist. Geol. Univ. Padova, vol. 3, Mem. 1, pp. 143, 255 (middle Eocene, northern Italy).

*Terebellum (Seraphs) pliciferum* Bayan, Bayan, 1870, Études faites dans la collection de l'École des Mines sur des fossiles nouveaux ou mal connus. Fasc. 1. Mollusques tertiaires. Paris; p. 49, pl. 8, figs. 1, 2 (middle Eocene, northern Italy).

*Terebellum (Mauryna) pliciferum* Bayan, de Gregorio, 1896, Ann. Géol. Paléont., livraison 21, p. 36 (middle Eocene, northern Italy); Cossmann, 1904, Essais de paléoconchologie comparée, livraison 6, p. 47, pl. 5, fig. 10 [middle Eocene, northern Italy; *not* Priabonian (Oligocene) as stated by Cossmann]; Dainelli, 1904, Palaeont. Italica, vol. 10, p. 162

*Terebellum (Mauryna ?) pliciferum* Bayan, Dainelli, 1905, Palaeont. Italica, vol. 11, pp. 76, 92, pl. 2, fig. 6 (middle Eocene, Yugoslavia).

*Mauryna plicifera* Bayan, de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi, Palermo, p. 25, pl. 1, fig. 28, pl. 5, fig. 31 (middle Eocene, northern Italy).

*Mauryna plicifera transeuns* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi, Palermo, p. 25, pl. 5, fig. 23 (middle Eocene, northern Italy).

*Mauryna protoelegans* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi, Palermo, p. 24, pl. 1, figs. 25, 26, pl. 5, fig. 30 (middle Eocene, northern Italy).

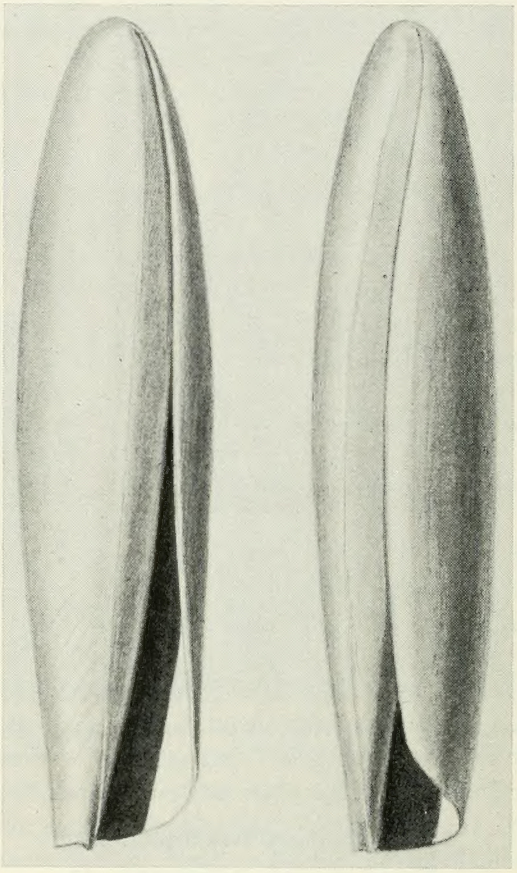
? *Terebellum (Mauryna) pliciferum* Bayan, Doncieux, 1908, Ann. Univ. Lyon, n.s., I. Sci., Méd., fasc. 22, p. 93, pl. 4, figs. 16a, 16b (late Paleocene, southern France).

*Description.* — Of medium size; moderately slender. Surface sculptured by axial swellings of somewhat variable width. The axials are parallel to the growth lines, *i.e.* slightly undulating. Outer lip not thickened. Callus of inner lip thin.

*Lectotype (herewith selected).* — Specimen figured by Bayan (1870b, pl. 8, fig. 1), which is deposited at the Ecole des Mines de Paris, Laboratoire de Paléontologie, No. G 2100.

*Dimensions of lectotype.* — Height 33.7 mm; maximum diameter 13.9 mm.

*Type locality.* — Croce Grande near San Giovanni Ilarione, northern Italy. Lutetian (middle Eocene).



Text-figure 17. Two views of *Seraphs leukoleptus* Jung. Paratype from the Lutetian of Chaussy. Ecole des Mines de Paris, Laboratoire de Paléontologie, unnumbered. Coll. Deshayes; 5 ×.

Except the lectotype the collections of the Ecole des Mines de Paris, Laboratoire de Paléontologie, contain two paralectotypes of *S. plicifer*. The larger specimen (Pl. 7, figs. 1-4) was figured by Bayan (1870b, pl. 8, fig. 2) and was collected at Pozza near San Giovanni Ilarione, *i.e.* near the type locality. This specimen was originally attached to a piece of matrix like the lectotype. The smaller paralectotype (Pl. 7, fig. 8), which was collected at the type locality, is not attached to matrix. It is an immature specimen, but its axial swellings are already well developed, *i.e.* they are not much smaller than those of the lectotype and the larger paralectotype.

*Measurements (in mm).* — All the measured specimens were collected from the type area.

| height | diameter | ratio |
|---|---|---|
| 33.7 | 13.9 | 2.4 |
| 36.0 | 14.2 | 2.5 |
| 38.7 | 14.5 | 2.7 |
| 43.5 | 16.4 | 2.6 |
| 43.8 | 16.0 | 2.7 |

As will be seen later *S. plicifer* is not a species of *Mauryna* but a true *Seraphs*. Although its axial sculpture is unique, it seems to be related to *S. sopitus*. The same type of sculpture has been observed on shells of *S. sopitus* from the Lutetian of Grignon near Paris. But on those shells the axials are weaker and seem to represent merely accentuated growth lines (see Pl. 1, figs. 16-17).

The strength of the axial sculpture is variable to some degree. Large suites of specimens might even show that there is a gradual transition from unsculptured *S. sopitus* to sculptured *S. plicifer*. De Gregorio (1880, p. 25) discussed the variability of the intensity of the axial sculpture and introduced the names *protoelegans* and *transeuns* for different stages.

*Distribution.* — Late Paleocene, southern France (?). Middle Eocene: northern Italy, Yugoslavia.

### **Seraphs (Seraphs) minus** (Vincent)

Plate 6, figures 9-10

*Terebellum (Seraphs) minus* Vincent, 1913, Ann. Mus. Congo Belge, ser. 3, vol. 1, p. 19, pl. 1, figs. 23, 24 (Paleocene of Landana, Cabinda, Angola).

*Type.* — Vincent (1913, p. 19) based his *S. minus* on two small specimens, which could not be found during a visit to the Musée de l'Afrique Central in Tervuren, Belgium, on August 3, 1966.

*Type locality.* — The type specimens were found in a block of the Landana beds (Paleocene) at Landana (Cabinda, Angola).

The type specimens of *S. minus* are the only ones of the species recorded. They are not satisfactory as type material because of their small size (height about 8 mm). Judging from the original figures they represent the immature stage of some species of *Seraphs*. It is, therefore, proposed to treat *S. minus* as a *nomen dubium*, but it is nevertheless interesting to have the genus *Seraphs* recorded as far south as Angola.

### **Seraphs (Seraphs) belemnitus** Palmer

Plate 6, figures 11-16

*Terebellum (Seraphs) belemnitum* Palmer, *in* Richards and Palmer, 1953, Florida Geol. Sur., Bull. No. 35, p. 25, pl. 3, figs. 9, 12 (upper Eocene, Florida); Palmer and Brann, 1966, Bull. Amer. Paleont., vol. 48, No. 218, p. 946.

? *Terebellum (Seraphs) belemnitum* Palmer ?, Woodring, 1959, U.S. Geol. Sur., Prof. Paper 306-B, p. 192, pl. 25, fig. 6 (late Eocene, Panamá Canal Zone).

*Description.* — Of medium to large size, cylindrical, slender. Outer lip somewhat thickened, straight, *i.e.* the growth lines are not undulating. Callus of inner lip moderately well developed. Base of available specimens not preserved.

*Holotype.* — Florida Geol. Survey, No. I-7642.

*Dimensions of holotype.* — Height 49 mm; maximum diameter 15 mm.

*Type locality.* — Florida Geol. Survey locality L-93: a road metal pit 2.9 miles south of the north limits of the town of Gulf Hammock just southwest of State Road 55 in the southwest quarter of Section 34, Township 14 South, Range 16 East. Inglis member of Moodys Branch Formation (late Eocene).

Due to the kindness of S. R. Windham of the Florida Geological Survey, Tallahassee, it was possible to study artificial casts of the type specimens. A cast of the holotype is here figured (Pl. 6, fig. 11). The state of preservation of the type specimens, however, is such that they are not instructive. Two better specimens from the type locality, which are more complete, were kindly made available for study by Dr. K. V. W. Palmer of Ithaca, N.Y. (see Pl. 6, figs. 12-16).

An artificial cast of the specimen from the late Eocene Gatuncillo Formation of the Panamá Canal Zone figured by Woodring (1959, pl. 25, fig. 6) is at hand. This specimen is too incomplete for a definite identification.

*S. belemnitus* with its involute spire obviously is a species of *Seraphs*. However, its slender cylindrical shape is not characteristic for that genus but recalls species of *Paraseraphs*. In this respect *S. belemnitus* is similar to *S. leukoleptus* from the middle Eocene of the Paris Basin, although the latter is a much smaller form. Complete specimens of *S. belemnitus* would be about 60 mm high, *i.e.* about twice as large as *S. leukoleptus*.

*Distribution.* — Late Eocene, Florida, Panamá Canal Zone (?).

### **Seraphs (Seraphs) squamosus** (Martin)

Plate 6, figures 17-19

*Terebellum (Seraphs) squamosum* Martin, 1914, Sammlungen Geol. Reichs-Museums Leiden, Neue Folge, Bd. 2, Heft 4, p. 160, pl. 5, figs. 125, 126 ("upper Eocene", Java); Martin, 1931, Wetenschappelijke Meded., No. 18, p. 38 ("upper Eocene", Java).

*Terebellum squamosum* Martin, van der Vlerk, 1931, Leidsche Geol. Meded., deel 5, p. 248 ("upper Eocene", Java).

*Description.* — Of medium size. Spire stout but pointed. Level of greatest diameter situated at about the adapical end of the aperture. Body whorl slightly concave on lower half. Columella slightly bent to the left and backwards. Callus on inner lip well developed, reaching up to the apex. Outer lip slightly thickened and swinging backwards well above the base. Surface of immature specimens smooth except for a few faint spiral grooves near the apex. Adult specimens are sculptured on the lower half of the body whorl. The growth lines are crossed by more prominent grooves. These grooves are not continuous but more or less regularly set off at each intersection. This produces a more or less regular, reticulate pattern with a component in a spiral direction.

*Lectotype (herewith selected).* — Rijksmuseum van Geologie en Mineralogie, Leiden, No. St. 10344.

*Dimensions of lectotype.* — Height 37.1 mm; maximum diameter 13.1 mm.

*Type locality.* — Kali Puru, Nanggulan, Res. Djokjakarta, Java. "Upper Eocene".

The lectotype is the specimen figured by Martin on plate 5, figures 125-125c. In addition there are nine paralectotypes in the collection of the Rijksmuseum van Geologie en Mineralogie in Leiden. With the exception of one immature shell all have been collected at the type locality. The spire is rather pointed in adults, but less so in immature specimens. Although it is not constant, the sculptural pattern on the lower portion of the body whorl is characteristic for *S. squamosus*. Nothing comparable occurs in any other species of *Seraphs*.

*Distribution.* — "Upper Eocene", Java.

### **Seraphs (Seraphs) subconvolutus** (d'Orbigny)

Plate 8, figures 1-10, Text-figure 18

*Terebellum convolutum* Lamarck, Grateloup, 1833, Actes Soc. Linn. Bordeaux, vol. 6, p. 314 (Oligocene, southwestern France); Grateloup, 1840-1846, Conchyliologie fossile des terrains tertiaires du bassin de l'Adour (environs de Dax), pl. 42, fig. 1 (Oligocene, southwestern France).

*Terebellum fusiforme* Lamarck, Grateloup, 1833, Actes Soc. Linn. Bordeaux, vol. 6, p. 315 (Oligocene, southwestern France); Grateloup, 1840-1846, Conchyliologie fossile des terrains tertiaires du bassin de l'Adour (environs de Dax), pl. 42, figs, 2, 3 (Oligocene, southwestern France).

*Terebellum subconvolutum* d'Orbigny, 1850-1852, Prodrome de paléontologie . . ., vol. 3, p. 9, 1852 (Oligocene, southwestern France); Fuchs, 1870, Denkschr. K. Akad. Wiss. Wien, math.-naturwiss. Classe, vol. 30, p. 148 (Oligocene, northern Italy). Magne, 1940, Proc. verb. Soc. Linn. Bordeaux, vol. 91, p. 33 (Oligocene, southwestern France); Vergneau, 1967, Bull. Inst. Géol. Bassin d'Aquitaine, No. 3, pp. 203, 206 (Oligocene, southwestern France). Coletti, F., Piccoli, G., Sambugar, B., Dei Medici, M. C., 1973, Mem. Ist. Geol. Min. Univ. Padova, vol. 28, p. 9 (middle Oligocene, northern Italy).

? *Terebellum subconvolutum* d'Orbigny, Fabiani, 1915, Mem. Ist. Geol. Univ. Padova, vol. 3, Mem. 1, pp. 267, 271 (Oligocene, northern Italy).

*Terebellum subfusiformis (sic)* d'Orbigny, 1850-1852, Prodrome de paléontologie . . ., vol. 3, p. 9, 1852 (Oligocene, southwestern France).

? *Terebellum (Terebellum) subfusiforme* d'Orbigny ?, Sacco, 1893, I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte 14, p. 21, pl. 2, figs. 19a, 19b (lower Oligocene, northern Italy).

*Description.* — Of medium size, slender, cylindrical. Aperture long and narrow. Callus of inner lip thin. Outer lip slightly thickened, somewhat prosocyrt below adapical end of aperture. Above the adapical end of the aperture the outer lip does not continue directly toward the apex, but runs in an antispiral direction reaching the apex after about half a volution. Columella slightly bent backwards near base.

*Holotype.* — Laboratoire de Géologie de Bordeaux, unnumbered (see also discussion below).

*Dimensions of holotype.* — Height (incomplete) 28 mm; maximum diameter 6.5 mm.

*Type locality.* — Gaas, Aquitaine Basin, France. Stampian (Oligocene).

Grateloup (1833, pp. 314, 315) described and figured *Terebellum convolutum* and *Terebellum fusiforme* from the Stampian of the same locality in the Gaas area, Aquitaine Basin. D'Orbigny (1850-1852, p. 9, 1852) found these forms to be different from the species of that name occurring in the Eocene of the Paris Basin, and renamed them *subconvolutum* and *subfusiforme* respectively. Magne (1940, p. 33) examined Grateloup's original specimens and found them to be conspecific. He correctely used the name *subconvolutum* as that name was listed first by D'Orbigny. According to written communication from A. M. Vergneau-Saubade of the Muséum d'Histoire Naturelle de Bordeaux the type lots of Grateloup's *T. convolutum* and *T. fusiforme* consist of a single specimen each which are deposited in the Laboratoire de Géologie de Bordeaux. They, therefore, represent the holotypes of *S. subconvolutus* and *S. subfusiformis* respectively. The holotype of *S. subconvolutus* is in a bad state of preservation (it was probably damaged after Grateloup studied it), and no photographs of it are available. It is nevertheless considered as the holotype of the species as here interpreted. The holotype of *S. subfusiformis* on the other hand is well preserved (see Pl. 8, fig. 1). In addition to these specimens there are five virtual topotypes in the Neuville collection, which is housed at the Institut de Géologie du Bassin d'Aquitaine, Talence, Gironde, France. Two of these shells are figured here (Pl. 8, figs. 2-5).

I am greatly indebted to Mrs. Vergneau-Saubade, Bordeaux, for information on and photographs of this species.

*S. subconvolutus* is a rare species. It was cited by Grateloup (1833, pp. 314, 315) from Lesbarritz, Gaas, and Lesperon, and by Magne (1940, p. 33) from the "Calcaire à Astéries" of La Souys. According to Vergneau (1967) all these localities are referred to the Stampian. The species has also been recorded from the Oligocene of northern Italy by Sacco (1893, p. 21) and Fabiani (1915, pp. 267, 271). Sacco referred internal casts from the Tongriano of Cassinelle to this species with doubt only. Two somewhat deformed internal casts from the same locality here figured (Pl. 8, figs. 11-12) are identified as *Seraphs* cf. *subconvolutus*. Fabiani listed *S. subconvolutus* from the Lattorfiano and Rupeliano of the Veneto, northern Italy. Two specimens contained in the Mayer-Eymar collection from the Oligocene of Castelgomberto (see Pl. 8, figs. 6-10) confirm the occurrence of *S. subconvolutus* in northern Italy.

*Measurements (in mm).* —

| height | diameter | ratio |
|---|---|---|
| 28 | 6.5 | 4.3 |
| 28 | 7 | 4.0 |
| 29 | 7 | 4.1 |
| 29 | 7.5 | 3.9 |
| 30 | 7 | 4.3 |
| 38 | 9 | 4.2 |
| 39 | 9.5 | 4.1 |

*S. subconvolutus* is characterised by the opisthocline continuation of the outer lip on the spire and its slender general shape which recalls species of the genus *Paraseraphs*. The same features are shown by *S. naricus* (Vredenburg) from the Oligocene of Pakistan. Considering the fact that *S. subconvolutus* and *S. naricus* both have a restricted occurrence in distant areas, it is not certain that they are closely related. They possibly represent a case of convergence.

*Distribution.* — Stampian (Oligocene), Aquitaine Basin, France. Oligocene of northern Italy.

### **Seraphs (Seraphs) mayeri,** n. sp.

Plate 8, figures 13-21, Text-figure 18

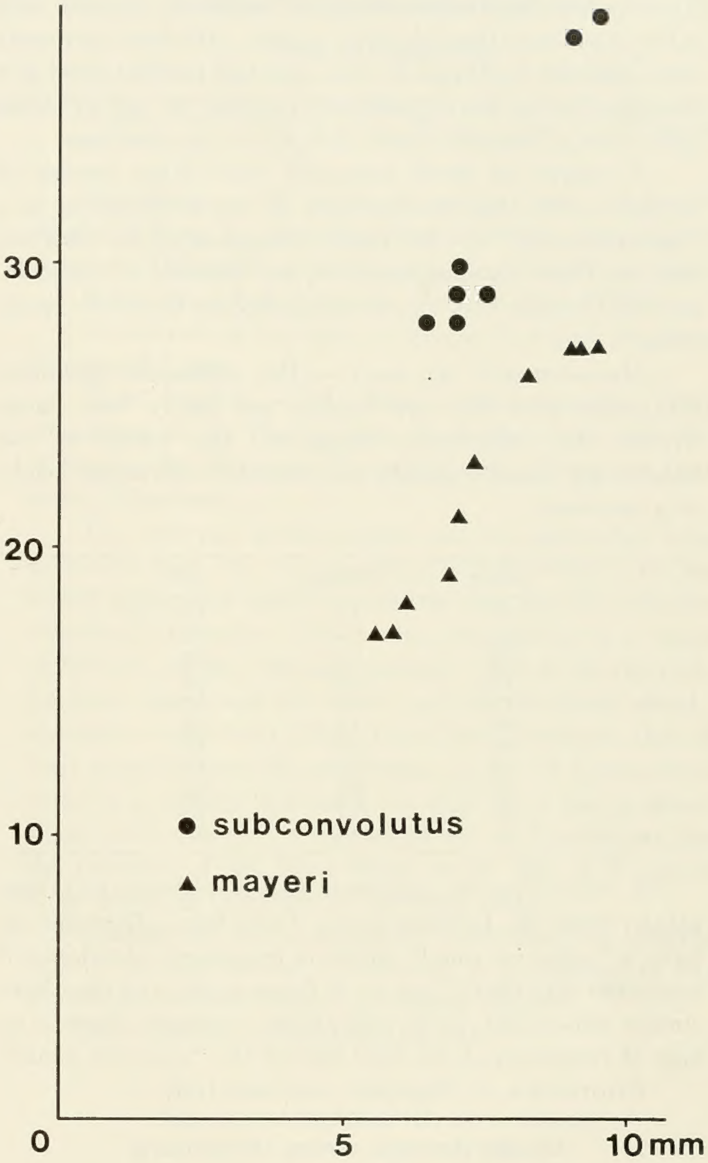
*Description.* — Of small to medium size, moderately slender. Apex moderately pointed. Inner lip thin, continuing above the adapical end of the aperture up to the apex. Outer lip thin except on spire, where it is slightly thickened and forms a "posterior canal". The shell of the body whorl behind this "canal" is usually somewhat resorbed and thus becomes transparent, with the result that the sutures of earlier whorls are visible. Columella slightly bent backwards near base.

*Holotype.* — Naturhistorisches Museum Basel, No. H 16578.

*Dimensions of holotype.* — Height 21.4 mm; maximum diameter 7.3 mm.

*Type locality.* — Monte Grumi near Castelgomberto, northern Italy. Oligocene.

This species is based on 15 specimens from the type locality and 16 specimens from the Oligocene of Santa



Text-figure 18. Graph showing height/diameter relationships of *S. subconvolutus* and *S. mayeri*.

Trinità near Montecchio Maggiore which is situated only a few kilometers from the type locality. All these specimens were collected by Mayer-Eymar, who had labelled them as a new species but never published it. None of the available specimens is complete; they all lack the extreme base.

*S. mayeri* is small compared with other species of *Seraphs s. str.* It is characterised by the development of a "posterior canal" and the partial resorption of the shell behind it. These features, however, are variable to some degree, but usually they can be recognized on immature specimens.

*Measurements (in mm).* — The measured specimens are partly from the type locality and partly from Santa Trinità near Montecchio Maggiore. The values of the heights are restored and do not represent the actual height of a specimen.

| height | diameter | ratio |
|---|---|---|
| 17 | 5.6 | 3.0 |
| 17 | 5.9 | 2.9 |
| 18 | 6.1 | 2.9 |
| 19 | 6.9 | 2.8 |
| 21 | 7.0 | 3.0 |
| 23 | 7.3 | 3.1 |
| 24 | 7.6 | 3.2 |
| 26 | 8.2 | 3.2 |
| 27 | 9.0 | 3.0 |
| 27 | 9.1 | 3.0 |
| 27 | 9.4 | 2.9 |

*S. mayeri* can be compared with *S. chilophorus* (Cossmann) from the Lutetian of the Paris Basin. Both species have a "posterior canal" which is imperfectly developed if compared with that of species of *Paraseraphs*, and they have similar dimensions. In *S. chilophorus*, however, there is no sign of resorption of the shell behind the "posterior canal".

*Distribution.* — Oligocene, northern Italy.

### **Seraphs (Seraphs) naricus** (Vredenburg)

Plate 6, figures 20-22

*Terebellum (Seraphs) naricum* Vredenburg, 1925, Mem. Geol. Sur. India, vol. 50, pt. 1, p. 323, pl. 13, figs. 4a, 4b, 4c (Oligocene, Sind).

*Description.* — Of medium size, slender, cylindrical. Apex moderately pointed. Aperture long and narrow. Callus on inner lip not preserved. Outer lip thin, prosocyrt near the adapical end of the aperture, but opisthocline on spire. Base of columella broken.

*Holotype.* — Central Palaeont. Labs., Geol. Sur. of India, Calcutta, No. 12614.

*Dimensions of holotype.* — Height 38.6 mm; maximum diameter 10.8 mm.

*Type locality.* — Bhagothoro Hill, Sind, Pakistan. Nari beds (Oligocene).

*S. naricus* is so far known only from one specimen, the holotype. I am greatly obliged to Dr. M. V. A. Sastry of the Geological Survey of India, Calcutta, who sent photographs and artificial casts of the holotype. According to written communication from Dr. S. S. Sarkar of the Geological Survey of India, Calcutta, *S. naricus* has been collected from the Lower Nari Series, but the exact horizon cannot be determined. In his letter dated June 15, 1968, Dr. Sarkar further stated: "The Nari Series as a whole is considered to be Oligocene. The lower part of the Lower Nari, which is characterised by the presence of *Nummulites fichteli*, is of Lattorfian age, whereas the upper part with its characteristic *Lepidocyclina (Eulepidina) dilatata* and *N. fichteli* is considered as Stampian". According to Nagappa (1959) the Nari beds are Oligocene, and Eames (1970, pp. 38, 43) considered the Lower Nari of Pakistan to be of Rupelian (middle Oligocene) age.

*S. naricus* together with *S. subconvolutus* (d'Orbigny) is one of the youngest species of *Seraphs*. The spire is entirely covered by the body whorl, but the general shape is not typical for *Seraphs*. The slenderness of *S. naricus* reminds one of species of *Paraseraphs* or *Terebellum*. The opisthocline direction of the outer lip on the spire can possibly be interpreted as a transitional stage to the genus *Terebellum*. If this is so, *S. naricus* could represent an ancestral form of *T. obtusum* J. de C. Sowerby from the lower or middle Miocene Gaj beds of Cutch, India.

*Distribution.* — Lower or middle Oligocene, Pakistan.

### **Seraphs (Seraphs) striatus** (von Koenen)

Plate 9, figures 1-4

*Terebellum striatum* von Koenen, 1889, Abhandl. geol. Specialkarte Preussen, Bd. 10, Heft 1, p. 39, pl. 1, figs. 7a, b, c, d (Lower Oligocene, Germany).

? *Terebellum striatum* von Koenen ?, von Koenen, 1894, Abhandl. königl. preuss. geol. Landesanstalt, Bd. 10, Heft 6, p. 1367.

*Description.* — Of medium size, slender. Surface smooth except for fine spirals on the lower part of the body whorl. Callus of inner lip well developed; it reaches up the spire toward the apex. Outer lip slightly thickened; it extends up to the apex. Columella slightly bent backwards near base.

*Type.* — Von Koenen (1889, p. 39) had two specimens at hand when he described this species. Besides the figured specimen, which measures 38.5 mm in height and 10.7 mm in diameter, he had a second, somewhat larger shell from the same locality. According to written communication from

Prof. K. Schmidt, Director of the Zentrales Geologisches Institut of the German Democratic Republic, the types and figured specimens of Von Koenen's (1889) paper have not been found after 1945 and have to be considered as lost. A neotype of *S. striatus* should, therefore, be selected. For the time being, however, no specimens of *S. striatus* are available, not even at the Museum für Naturkunde of the Humboldt University, East Berlin.

*Type locality.* — Lattorf, Germany. Lower Oligocene.

*S. striatus* is also a slender species of *Seraphs* like the Oligocene *S. subconvolutus* and *S. naricus*. But unlike those species the posterior part of its outer lip is practically straight and not opisthocline.

### **Seraphs (Seraphs) andersoni** Dickerson

Plate 9, figures 5-6

*Seraphs andersoni* Dickerson, 1917, Calif. Acad. Sci., Proc., ser. 4, vol. 7, No. 6, p. 180, pl. 31, figs. 9a, 9b (Lower Oligocene, Washington); Van Winkle, 1918, Univ. Washington Publ. Geol., vol. 1, No. 2, p. 76 (Lower Oligocene, Washington).

*Terebellum andersoni* (Dickerson), Effinger, 1938, Jour. Paleont., vol. 12, No. 4, p. 380 (Lower Oligocene, Washington).

*Description.* — Of medium size, moderately stout. Apex pointed. Surface smooth. Growth lines slightly prosocyrt. Inner lip thin. Outer lip not thickened. Columella somewhat bent backwards near base.

*Holotype.* — California Academy of Sciences, Dept. of Geology, San Francisco, No. 434.

*Dimensions of holotype.* — Height 38 mm; maximum diameter 11 mm.

*Type locality.* — California Academy of Sciences Locality 181: "near Vader, Lewis County, Washington; on the east bank of the Cowlitz River, just back of the Greeco ranch house, about four miles east of Vader". Lower Oligocene (*Molopophorus lincolnensis* Zone).

The two specimens of *S. andersoni* recorded by Dickerson (1917) apparently are the only ones reported in literature. The original figures show a suture on the spire. This suture, however, is not present on the type specimens (see Pl. 9, figs. 5-6). The late Dr. L. G. Hertlein of the California Academy of Sciences wrote the following about the holotype (letter dated November 18, 1965): "We have examined the type specimen of *Seraphs andersoni* and it appears to us that no suture is present. Erosion in some spots gives the illusion of a suture, but on uneroded areas no suture is present". In addition L. G. Hertlein sent an artificial cast of the paratype, on which no trace of a suture is recognizable. Contrary to the statement by Effinger (1938, p. 381). *S. andersoni* obviously is a species of *Seraphs*.

*Distribution.*—Lower Oligocene, Washington (U.S.A.).

### **Seraphs (?) hernandoensis** (Mansfield)

Plate 9, figures 7-9

*Terebellum hernandoensis* (*sic*) Mansfield, 1937, Florida Dept. Conservation, Geol. Bull. No. 15, p. 146, pl. 5, figs. 2, 3 (Oligocene, Florida).

*Description.* — Of small to medium size, moderately slender. Outer lip not thickened. Growth lines slightly prosocyrt. Columella somewhat bent backwards near base.

*Holotype.* — U.S. National Museum, No. 495948.

*Dimensions of holotype.* — Height 31.4 mm; maximum diameter 9.5 mm.

*Type locality.* — U.S. Geol. Survey locality 12318: abandoned pit on Florida State Road No. 15; 5 miles west of Brooksville, Hernando County, Florida. Suwannee Limestone (Oligocene).

The holotype of this species and two somewhat larger specimens from the type locality (USNM 645465) are preserved as internal casts. Apparently they are the only ones recorded in literature. This form is thought to be a species of *Seraphs* for the following reasons: there is no trace of a posterior canal and the lower part of the body whorl is somewhat constricted. There is no proof, however, that the body whorl covered the entire spire. If *S.* (?) *hernandoensis* really is a species of *Seraphs*, it may have had a general shape similar to that of *S. chilophorus* or *S. olivaceus* from the Lutetian of the Paris Basin, or to that of *S. mayeri*, n. sp. from the Oligocene of northern Italy.

Considering the uncertainties concerning the morphology of this species and its affinities, it is proposed to treat *Terebellum hernandoensis* as a *nomen dubium*.

*Distribution.* — Oligocene, Florida.

### Subgenus **MINISERAPHS**, new subgenus

Type species: *Terebellum (Seraphs) eratoides* Cossmann. Middle Eocene, Paris Basin, France.

*Description.* — Shell small, involute, of stout appearance. Apical angle large. Line of greatest diameter situated above the middle of the height of the shell. Surface of shell smooth except for indistinct growth lines and a few faint, oblique grooves near the base of the columella. Callus on inner lip thin. Outer lip somewhat thickened, sinuous. Stromboid notch rudimentary. Columella slightly bent backwards near base.

*Miniseraphs* — as the name implies — comprises small forms of *Seraphs* which so far are known to have a restricted stratigraphic and geographical distribution. *Miniseraphs* is distinguished from *Seraphs s. str.* not only by its much smaller size but also by its different proportions, *i.e.* its stout appearance and the larger apical angle.

*Miniseraphs* appears to represent a local offspring of *Seraphs s. str.* which so far is composed only of the two species *eratoides* and *isabella.* Another offspring of *Seraphs s. str.*, which lived at the same time as *Miniseraphs* and which appears to be related with it, is *Diameza. Diameza* has an even more restricted stratigraphic and geographical distribution being represented by its type species *intermedius* only, which has been found only at two localities of the Lutetian of the Paris Basin.

*Range.* — Middle Eocene: Paris Basin, northern Italy, Hungary.

### **Seraphs (Miniseraphs) eratoides** (Cossmann)

Plate 9, figures 10-12, Text-figures 19, 20

*Terebellum (Seraphs) eratoides* Cossmann, 1889, Ann. Soc. Roy. Malac. Belgique, vol. 24, p. 98, pl. 3, figs. 7, 8 (Lutetian, Paris Basin); Cossmann and Pissarro, 1905, Bull. Soc. géol. Normandie, vol. 24, p. 97, pl. 16, fig. 36 (Middle Eocene of the Cotentin, France); Cossmann and Pissarro, 1906-1913, Iconographie complète des coquilles fossiles de l'éocène des environs de Paris, vol. 2, pl. 32, fig. 158-7, 1911 (Lutetian, Paris Basin).

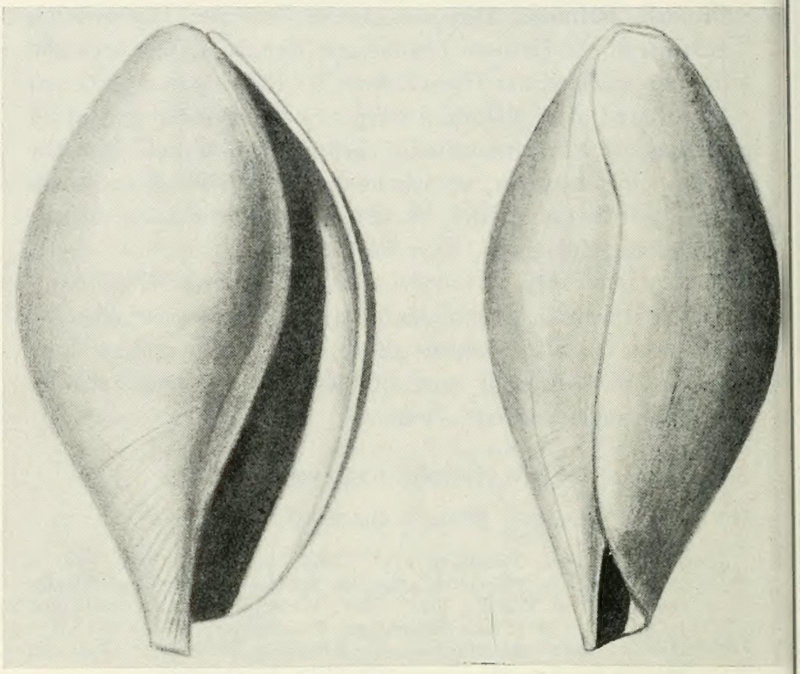
*Description.* — Of small size, stout. Apical angle large. Line of greatest diameter situated on upper part of shell. Callus of inner lip thin, inconspicuous. Outer lip slightly sinuous, thickened, but less so near base. Columella almost straight. Base of outer lip reaches almost down to the level of the base of the columella. Sculpture consists of a few faint, spiral grooves near the base.

*Type.* — Cossmann's original figure represents a specimen from Chaussy collected by Bernay. This specimen should be selected as the lectotype. It has not been found in the collections of the Ecole des Mines de Paris, Laboratoire de Paléontologie.

*Type locality.* — Chaussy, Dept. Seine-et-Oise, France. Lutetian (middle Eocene).

*S. eratoides* is a rare species. I have seen only six specimens, all of them from the type locality. Five are contained in a lot collected by Bourdot which is deposited at the Ecole des Mines de Paris, Laboratoire de Paléontologie. The sixth shell (see Pl. 9, figs. 10-12) is from the collection of Mayer-Eymar. As explained under *Diameza S. eratoides* or its immediate ancestor probably gave rise to *Seraphs (Diameza) intermedius* (Deshayes), the type species of *Diameza.*

*Measurements (in mm).* — All the measured specimens are from Chaussy, the type locality (see Text-figure 20).



Text-figure 19. Two views of *Seraphs (Miniseraphs) eratoides* from the Lutetian of Chaussy. Ecole des Mines de Paris, Laboratoire de Paléontologie, unnumbered. Coll. Bourdot; 12 ×.

| height | diameter | ratio |
|---|---|---|
| 6.9 | 3.9 | 1.8 |
| 7.0 | 3.9 | 1.8 |
| 7.2 | 4.2 | 1.7 |
| 7.5 | 4.3 | 1.7 |
| 8.0 | 4.5 | 1.8 |
| 8.1 | 4.6 | 1.8 |

At first glance *S. eratoides* seems to be a minature *S. isabella.* However, *S. eratoides* reaches only about half the size of *S. isabella,* and it is somewhat stouter. Immature *S. isabella* is much more slender than adult *S. eratoides.*

*Distribution.* — Lutetian (middle Eocene) of Paris Basin, France.

### **Seraphs (Miniseraphs) isabella** (Deshayes)

Plate 9, figures 13-18, Text-figures 20, 21

*Terebellum isabella* Bernay, Deshayes, 1864-1865, Description des animaux sans vertèbres découverts dans le bassin de Paris, vol. 3, p. 470; Atlas, pl. 92, figs. 14, 15, 1865 (Lutetian, Paris Basin); Oppenheim, 1896, Palaeontographica, vol. 43, p. 195 (part: not the large specimens = small *superbum* de Gregorio = ? *sopitus* (Solander)) (middle Eocene, northern Italy); Fabiani, 1915, Mem. Ist. Geol. Univ. Padova, vol. 3, Mem. 1, p. 255 (middle Eocene, northern Italy).

*Terebellum (Seraphs) isabellae* Bernay, Cossmann, 1889, Ann. Soc. Roy. Malac. Belgique, vol. 24, p. 98 (middle Eocene, Paris Basin); Cossmann and Pissarro, 1906-1913, Iconographie complète des coquilles fossiles de l'éocène des environs de Paris, vol. 2, pl. 32, fig. 158-6, 1911 (Lutetian, Paris Basin).

Not *Terebellum (Seraphs) isabellae* Bernay, Malaroda, 1954, Mem. Ist. Geol. Min. Univ. Padova, vol. 19, p. 58 (early Eocene, northern Italy).

*Terebellum pusilliusculum* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi, Palermo, p. 23, pl. 1, fig. 33 (middle Eocene, northern Italy).

*Terebellum (Seraphs) vertesensis (sic)* Szöts, 1953, Geologica Hungarica, ser. pal., fasc. 22, pp. 17, 57, 128, 175, pl. 4, figs. 43, 44 ("Lower Eocene", Hungary).

*Description.* — Of small size, rather stout. Apical angle large. Body whorl inflated. Line of greatest diameter situated a little above the middle of the height of the shell. Callus of inner lip thin; not preserved on most specimens. Outer lip sinuous, not thickened below, but somewhat thickened on upper part. Columella slightly bent backwards near base. Outer lip reaches almost down to the level of the base of the columella. Surface of shell smooth except for growth lines and a few faint, spiral grooves near the base.

*Lectotype (herewith selected).* — Ecole des Mines de Paris, Laboratoire de Paléontologie, unnumbered. Coll. Bernay. The lectotype is a somewhat incomplete shell: the outer lip is not complete and a little piece at the base is missing. The original figure is an idealised drawing, and it is, therefore, impossible to make out, which was the specimen Deshayes actually figured.

*Dimensions of lectotype.* — Height 13.4 mm; maximum diameter 7.0 mm.

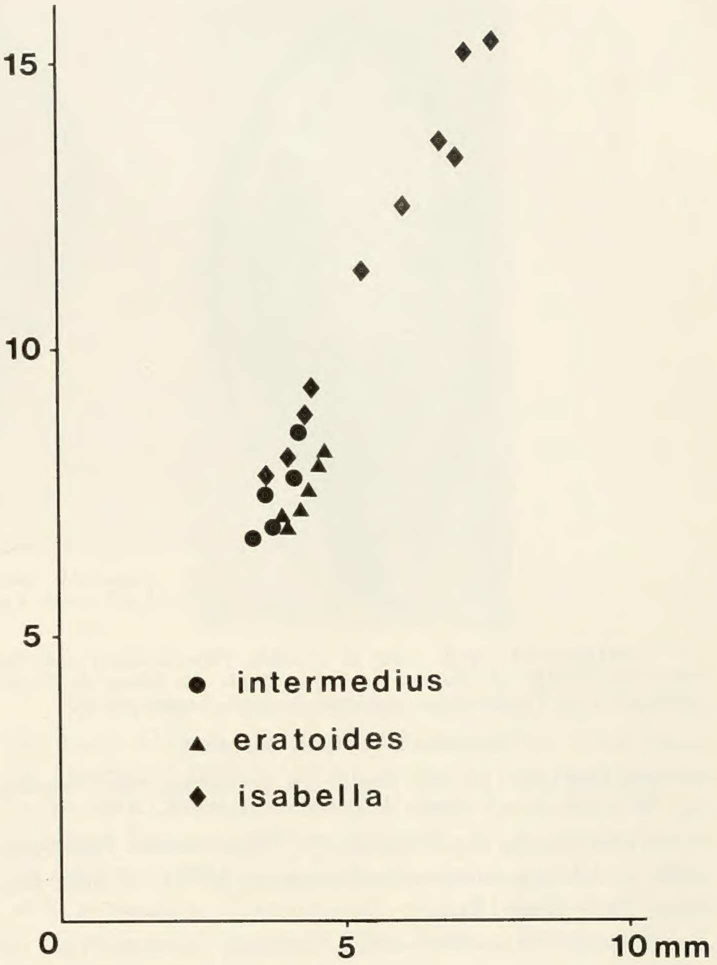
*Type locality.* — Chaussy, Dept. Seine-et-Oise, France. Lutetian (middle Eocene).

Although this taxon was first published in the combination *Terebellum isabella* Bernay, Deshayes, who is the author of the whole work, is the author of this species. The later emendation of *isabella* to the genitive *isabellae* is correct, but unnecessary, because *isabella* can well be used as a noun in the nominative.

This species occurs at several localities in the Paris Basin (Chaussy, Mouchy, Fercourt, Ferme de l'Orme, Grignon, Parnes, Liancourt, Vaudancourt), and stratigraphically it seems to be restricted to the Lutetian.

*Seraphs vertesensis* (Szöts) (1953, p. 175) was described from beds assigned to the lower Eocene (according to personal communication from H. Schaub these beds are probably of middle Eocene age). Its dimensions and proportions are the same as those of *S. isabella.* Both specimens figured by Szöts are immature, even the larger one, the outer lip of which does not seem to be thickened. Szöts separated *S. vertesensis* from *S. isabella* because of the shape of the growth lines. The shells of *S. isabella* examined, however, show that this feature is variable to some degree, *i.e.* the outer lip is more or less sinuous (see Pl. 9, figs. 14, 17).

*Measurements (in mm).* — All the measured specimens are from Chaussy, the type locality (see Text-figure 20).

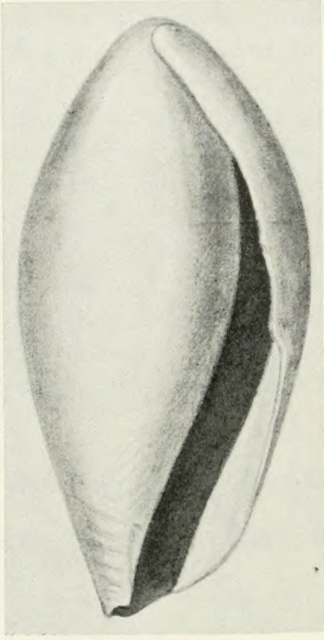


Text-figure 20. Graph showing height/diameter relationships of *S. intermedius, S. eratoides,* and *S. isabella.*

| height | diameter | ratio |
|---|---|---|
| 7.7 | 3.6 | 2.1 |
| 8.1 | 4.0 | 2.0 |
| 8.9 | 4.3 | 2.1 |
| 9.3 | 4.4 | 2.1 |
| 11.4 | 5.3 | 2.1 |
| 12.5 | 6.0 | 2.1 |
| 13.4 | 7.0 | 1.9 |
| 13.7 | 6.7 | 2.0 |
| 15.2 | 7.1 | 2.1 |
| 15.4 | 7.6 | 2.0 |

*S. isabella* can be compared with *S. eratoides* only. It is easily distinguished from that species by its larger size. *S. isabella* is more slender, *i.e. S. eratoides* is more constricted toward the base and thus has a stouter appearance. Immature shells of *S. isabella* are also more slender than *S. eratoides.*

*Distribution.* — Middle Eocene: France, northern Italy, Hungary.



Text-figure 21. Front view of *Seraphs (Miniseraphs) isabella* from the Lutetian of Chaussy. Lectotype. Ecole des Mines de Paris, Laboratoire de Paléontologie, unnumbered. Coll. Bernay; 6 ×.

### Subgenus **DIAMEZA** Deshayes

*Diameza* Deshayes, 1864-1865, Description des animaux sans vertèbres découverts dans le bassin de Paris, vol. 3, p. 572, 1865.

Type species (by monotypy): *Ovula media* Deshayes, 1865 (= *Ovula intermedia* Deshayes, 1837). Middle Eocene, Paris Basin, France.

*Description.* — Shell small, inflated, involute. Line of greatest diameter situated a little above the middle of the height of the shell. Surface smooth except for indistinct growth lines and a few faint, oblique grooves near the base of the columella. Parietal callus only weakly developed. Outer lip somewhat thickened and sinuous, *i.e.* prosocyrt on lower part and opisthocyrt on upper part of shell. The outer lip extends above the apex, where it forms a pointed structure which is hiding the actual apex. Stromboid notch rudimentary. Columella slightly bent backwards near base.

The type species of *Diameza* was originally described as a species of *Ovula*, and later it was assigned to the Cypraeidae. I agree with Cossmann (1904, pp. 47-48) that *Diameza* is more closely related to *Terebellum*, *i.e.* to *Seraphs*, and it is, therefore, treated here as a subgenus of *Seraphs*. *Diameza* shows the characteristic features of Seraphsidae and especially of *Seraphs*: the rudimentary stromboid notch, the shape of the growth lines, the practically smooth surface, and a columella, which is slightly bent backwards near the base. The only unusual character is the pointed structure on the apex.

As already pointed out by Cossmann the type species of *Diameza* is remarkably similar to *Seraphs eratoides* (Cossmann), the type species of *Miniseraphs* from the Lutetian of Chaussy, Paris Basin. In fact *Miniseraphs* is distinguished from *Diameza* only by the lack of a pointed structure on the apex. *S. intermedius* and *S. eratoides* probably had a common ancestor, which, however, is still unknown.

*Range.* — Lutetian (middle Eocene) of Paris Basin, France.

### **Seraphs (Diameza) intermedius** (Deshayes)

Text-figures 20, 22-25

*Ovula intermedia* Deshayes, 1824-1837, Description des coquilles fossiles des environs de Paris, vol. 2, p. 718, pl. 95, figs. 34, 35, 36, 1837 (middle Eocene, Paris Basin).

*Ovula media* Deshayes, 1864-1865, Description des animaux sans vertèbres découverts dans le bassin de Paris, vol. 3, p. 572, 1865 (Lutetian, Paris Basin). New name for *Ovula intermedia*.

*Diameza media* Deshayes, Cossmann, 1889, Ann. Soc. Roy. Malac. Belgique, vol. 24, p. 99, pl. 3, fig. 16 (middle Eocene, Paris Basin).

*Terebellum (Diameza) media* (Deshayes), Cossmann, 1904, Essais de paléoconchologie comparée. Sixième livraison, pp. 47-48, pl. 3, figs. 9-12 (Lutetian, Paris Basin).

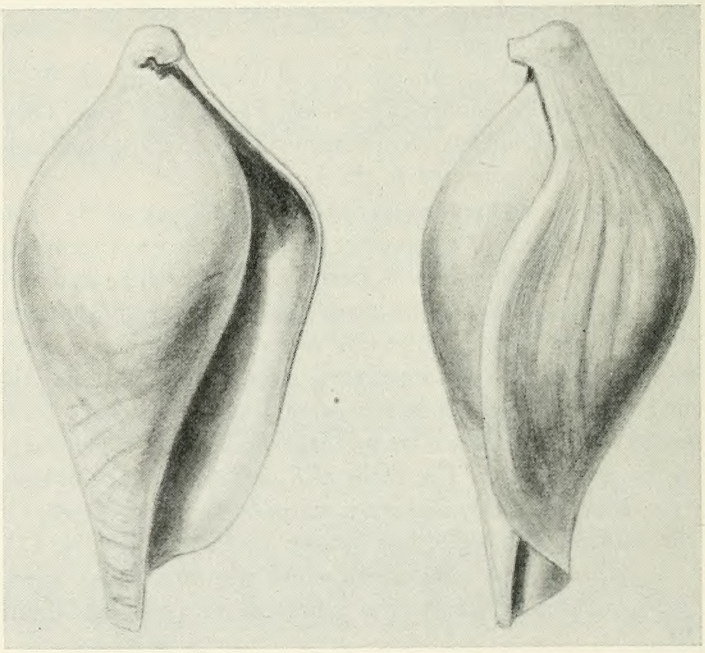
*Diameza media* (Deshayes), Cossmann and Pissarro, 1906-1913, Iconographie complète des coquilles fossiles de l'éocène des environs de Paris, vol. 2, pl. 32, fig. 159-1, 1911 (Lutetian, Paris Basin).

*Description.* — See description of *Diameza*.

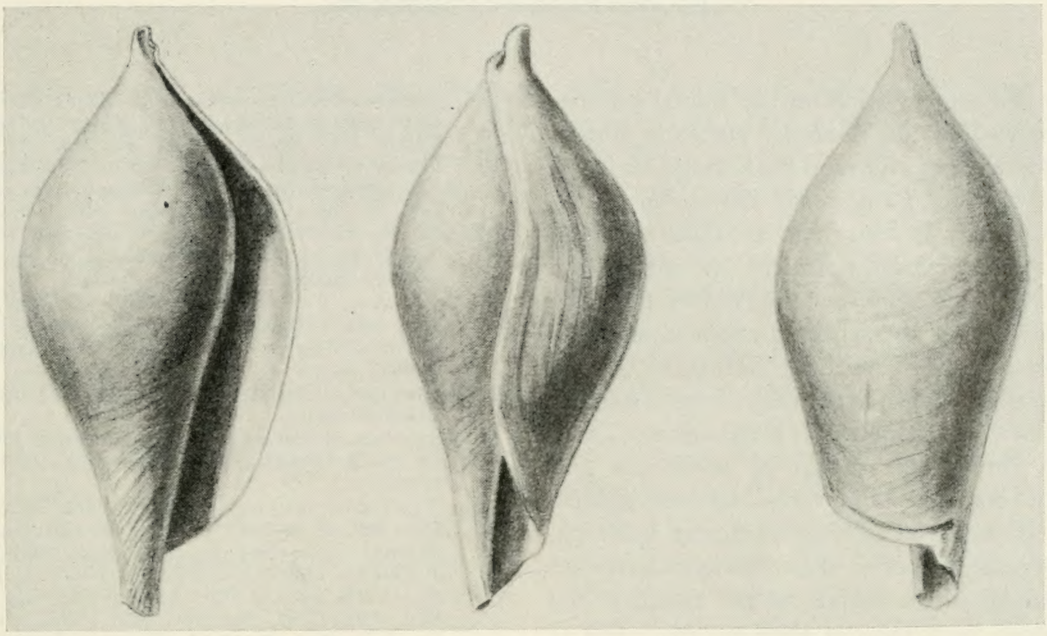
*Lectotype (herewith selected).* — Ecole des Mines de Paris, Laboratoire de paléontologie, No. G 2062.

*Dimensions of lectotype.* — Height 6.9 mm; maximum diameter 3.8 mm.

*Type locality.* — Grignon near Paris. Lutetian (middle Eocene).



Text-figure 22. Two views of the lectotype of *Seraphs (Diameza) intermedius*. Lutetian of Grignon near Paris. Ecole des Mines de Paris, Laboratoire de Paléontologie, No. G 2062; 12 ×.



Text-figure 23. Three views of *Seraphs (Diameza) intermedius* from the Lutetian of Grignon near Paris. Paralectotype. Ecole des Mines de Paris, Laboratoire de Paléontologie, No. G 2063; 12 ×.

The collections of the Ecole des Mines contain a lot with three specimens accompanied by the following label: "*Diameza media* Desh. Types de l'espèce, pl. 95, figs. 34, 35. Grignon. Coll. Deshayes 1867". Although the meaning of the number of the year is not clear, it certainly does not have to do anything with the date of collecting, because the original figure of this species was published long before that. The three specimens of this lot obviously represent the syntypes of the species. With the help of Deshayes' original drawing it is not possible to identify one of the three shells as the figured specimen. The lectotype is, therefore, the shell, which matches best the dimensions given by Deshayes (height 7 mm; diameter 4 mm). The two paralectotypes, one of which is immature, are numbered G 2063.

Another lot in the collections of the Ecole des Mines, which was collected by Caillat at Grignon, contains three adult and one immature shells which evidently are the specimens figured by Cossman (1904, pl. 3, figs. 9-12). One of them is refigured here (Text-figure 25). Two fragmentary specimens from Grignon are deposited at the Muséum National d'Histoire Naturelle in Paris (No. B 63255).

*Measurements (in mm).* — All the measured specimens were collected at Grignon, the type locality (see Text-figure 20).

| height | diameter | ratio |
|---|---|---|
| 6.6 | 3.3 | 2.0 |
| 6.9 | 3.8 | 1.8 |
| 7.6 | 3.6 | 2.1 |
| 7.8 | 4.1 | 1.9 |
| 8.6 | 4.2 | 2.0 |

So far this species is known only from two Lutetian localities (Grignon, Ferme de l'Orme) of the Paris Basin. De Gregorio (1880, p. 27, pl. 6, fig. 8) described another species of *Diameza, D. deshayesi,* from the Lutetian of San Giovanni Ilarione, northern Italy. His original figure shows an internal cast which is more than twice as high as shells of *S. intermedius.* No specimens of that form are contained in the rich collections from San Giovanni Ilarione at hand, and for the time being it seems best to consider *D. deshayesi* as a *nomen dubium.*

*Distribution.* — Lutetian (middle Eocene), Paris Basin, France.

### Genus **PARASERAPHS**, new genus

Type species: *Paraseraphs tetanus,* n. sp. (= *Terebellum fusiforme* of authors, not of Lamarck). Cuisian (early Eocene) of Paris Basin, France.

*Description.* — Shell slender, cylindrical, evolute, smooth. Suture indistinct. Callus on inner lip moderately prominent. Growth lines moderately prosocyrt. Adapical part of outer lip is thickened and extends as a posterior canal toward the apex. Largest diameter of shell near base.

*Paraseraphs* is characterised by its slender shape and the posterior canal which extends from the adapical end of the aperture toward the apex. This gutter-like structure is probably a homologue and possibly even an analogue to the sutural gutter of the living *Terebellum terebellum* which is occupied by the long sutural filament. Concerning the function of the sutural filament Jung and Abbott (1967, p. 446) stated: "We presume that this exposed filament is tactile in function and serves to inform the animal whether the shell is fully buried or not. A similar gutter is present in the suture of the shell of the sand-burrowing Olividae".

The posterior canal of *Paraseraphs* shows some variability as to shape. It may be bent in an antispiral direction as in *P. tetanus*, n. sp., or form a straight line toward the apex as in *P. placitus*. This canal was observed by the early authors, who, however, did not attribute much significance to it. An exception is James Sowerby (1821, p. 158), who wrote that "the position of this canal might form a foundation to establish a new genus upon. . .". De Gregorio (1880) also felt that the Terebellinae should be subdivided and expressed this by distinguishing three distinct groups, among which the group of *Terebellum fusiforme* Lamarck.

The posterior canal, however, is not always clearly set off from the remainder of the surface of the spire, *i.e.* the suture may be hidden by a wash of shell material. This is the case in *P. propedistortus* (de Gregorio) which thus tends to be involute like species of *Seraphs*. On the other hand *P. propedistortus* has the slender, fusiform shape, which is typical for species of *Paraseraphs*. *P. propedistortus*, therefore, tends to unite characters of *Seraphs* and *Paraseraphs*. Similar counterparts in the genus *Seraphs* are *S. leukoleptus*, n. sp. and *S. chilophorus* (Cossmann). *S. leukoleptus* has a shape like species of *Paraseraphs* but is entirely involute like species of *Seraphs*, whereas *S. chilophorus* has a shape like species of *Seraphs* and shows indications of a canal on the spire (although restricted to the apical area) like species of *Paraseraphs*. This situation appears to demonstrate that the two genera are closely related through the three transitional species mentioned above.

*Range.* — Early to late Eocene: Western Europe, Egypt, tropical America, California. The ranges of the species of *Paraseraphs* are summarized below:

| | early Eocene | middle Eocene | late Eocene |
|---|---|---|---|
| *P. tetanus* | ——— | | |
| *P. armoricensis* | ——— | ——— | — —? |
| *P. placitus* | | ——— | ——— |
| *P. propedistortus* | | ——— | — —? |
| *P. procerus* | | ——— | — —? |
| *P. erraticus* | | ——— | — —? |

### **Paraseraphs tetanus**, n. sp.

Plate 9, figure 26; Plate 10, figures 1-10, Text-figures 12, 26-28

*Terebellum fusiforme* Lamarck, d'Orbigny, 1850-1852, Prodrome de paléontologie . . ., vol. 2, p. 314, 1850 (reference to Cuise-Lamotte); Deshayes, 1864-1865, Description des animaux sans vertèbres découverts dans le bassin de Paris, vol. 3, p. 470, 1865 (reference to Cuise-Lamotte); Mayer, 1866, Vierteljahrsschrift Naturf. Ges. Zürich, Jg. 11, pp. 319, 332 (reference to Cuise-Lamotte); Cossmann and Pissarro, 1906-1913, Iconographie complète des coquilles fossiles de l'éocène des environs de Paris, vol. 2, pl. 31, fig. 158-1, 1911 (Saint Gobain near Paris: Cuisian).

*Terebellum fusiforme* Deshayes, Cossmann, 1904, Essais de paléoconchologie comparée, sixième livraison, pl. 2, fig. 10; pl. 3, fig. 4 (Saint Gobain near Paris: Cuisian).

? *Terebellum (Terebellum) fusiforme* Lamarck, Glibert, 1938, Mém. Mus. Roy. Hist. Nat. Belgique, No. 85, p. 65, pl. 4, fig. 7 (Bartonian of Belgium); Bagmanov, 1966, Larger Foraminifera and mollusk fauna of the Eocene deposits of the Trans-Caucasus (Russian). Baku, p. 178, pl. 81, figs. 3, 4 ("middle Eocene" of the Trans-Caucasus).

? *Terebellum fusiforme* Lamarck, Doncieux, 1908, Ann. Univ. Lyon, n.s., I. Sci., Méd., fasc. 22, p. 91 (late Paleocene, southern France).

Not *Terebellum fusiforme* Lamarck, 1802, Ann. Mus. National Hist. Nat., vol. 1, p. 390. "Quoique ce fossile ne se trouve point à Grignon, je le crois des environs de Paris". [= internal mould of *Seraphs sopitus* (Solander)]; Lamarck, 1811, Ann. Mus. Hist. Nat. Paris, vol. 16 (for 1810), p. 302. ". . . la localité n'est pas bien connue". J. Sowerby, 1821, The Mineral Conchology of Great Britain, vol. 3, p. 157, pl. 287, lower figures (= *Paraseraphs placitus*, n. sp.); Lamarck, 1822, Histoire naturelle des animaux sans vertèbres, vol. 7, p. 411. ". . . la localité n'est pas bien connue"; Deshayes, 1824-1837, Description des coquilles fossiles des environs de Paris, vol. 2, p. 738, 1837. Atlas, pl. 95, figs. 30, 31 (= *Paraseraphs placitus*, n. sp.); Grateloup, 1833, Actes Soc. Linn. Bordeaux, vol. 6, p. 315 (Oligocene, southwestern France) [= *Seraphs subconvolutus* d'Orbigny)]; d'Orbigny, 1850-1852, Prodrome de paléontologie . . ., vol. 2, p. 314, 1850 (part); Deshayes, 1864-1865, Description des animaux sans vertèbres découverts dans le Bassin de Paris, vol. 3, p. 470, 1865 (part); Cossmann, 1889, Ann. Soc. Roy. Malac. Belgique, vol. 24, p. 96; de Gregorio, 1890, Ann. Géol. Paléont., livraison 7, p. 116, pl. 10, figs. 7-10; Newton, 1891, British Oligocene and Eocene Mollusca. . ., p. 97; de Gregorio, 1894, Ann. Géol. Paléont., livraison 14, pp. 7, 11, pl. 1, fig. 21; Vinassa de Regny, 1896, Palaeont. Italica, vol. 1, pp. 230, 259 (part); de Gregorio, 1896, Ann. Géol. Paléont., livraison 21, p. 36, pl. 3, fig. 5; Dainelli, 1904, Palaeont. Italica, vol. 10, p. 162; Dainelli, 1905, Palaeont. Italica, vol. 11, pp. 72, 92; Fabiani, 1915, Mem. Ist. Geol. Univ. Padova, vol. 3, pp. 143, 255, 262; Favre, 1918, Catalogue illustré de la collection Lamarck. Mollusques trachélipodes fossiles. Geneva, pl. 13, figs. 209a-b: Type specimen of *T. fusiforme* Lamarck, 1802, which is an internal mould of *Seraphs sopitus* (Solander, 1766).

Not *Terebellum fusiforme* Lamarck (*fusiformis* in explanation of plate), Grateloup, 1840-1846, Conchyliologie fossile des terrains tertiaires du bassin de l'Adour (environs de Dax), pl. 42, figs. 2, 3 (Oligocene, southwestern France) [= *Seraphs subconvolutus* (d'Orbigny)].

Not *Terebellum fusiforme* Lamarck ?, d'Archiac and Haime, 1854, Description des animaux fossiles du groupe nummulitique de l'Inde, seconde livraison, p. 335, pl. 32, fig. 23.

Not *Terebellum (Seraphs) fusiforme* Lamarck, Tessier, 1952, Contributions à la stratigraphie et à la paléontologie de la partie Ouest du Sénégal (Crétacé et Tertiaire). Dakar, vol. 2, p. 374, pl. 32, figs. 16-18 (Lutetian of Senegal) [= ? *Seraphs olivaceus* (Cossmann)].

Not *Terebellum (Terebellum) fusiforme* Lamarck, Isaeva, 1933, Trans. United Geol. Prosp. Service USSR, fasc. 305, p. 30, pl. 3, fig. 10; Mészáros, 1957, Ed. Acad. Rep. Pop. Rumania, Mon. Geol. Paleont., No. 1, pp. 44, 142, pl. 8, figs. 1, 1a, pl. 28, figs. 2, 2a, 2b (part); Tolstikova, 1964, Mollusks from the Alaisk and Turkestansk beds of Badkhyz (Russian). Acad. Sci. USSR, Dept. Earth Sci., Dept. Monogr. Coll. A. P. Karpinski. "Nauka", Moscow-Leningrad, p. 78, pl. 2, figs. 12a, 12b.

Not *Terebellum* cf. *fusiforme* Lamarck, Cuvillier, 1933, Mém. Inst. Egypte, vol. 22, p. 46, pl. 5, figs. 16, 19 (upper Lutetian, Egypt) [= ? *Paraseraphs armoricensis* (Cossmann)].

*Description.* — Of medium size, slender. Protoconch consists of 1½ to 1¾ whorls. Postnuclear whorls 2½ to 3. Surface smooth. Callus of inner lip well developed. Outer lip not thickened. Posterior canal bent in an antispiral direction, usually not extending directly to the apex. Columella bent backwards near base. Outer lip does not reach down to the level of the base of the columella.

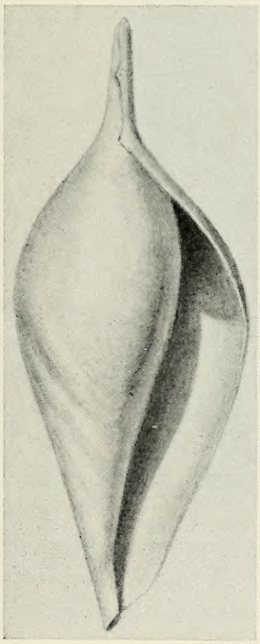
*Holotype.* — Naturhistorisches Museum Basel, No. H 15409.

*Dimensions of holotype.* — Height 28.7 mm; maximum diameter 7.1 mm.

*Type locality.* — Cuise-Lamotte, Dept. Oise, France. Cuisian (early Eocene).

The taxonomic history of this species is confusing, because *T. fusiforme* has been misunderstood by most writers. This situation is due to the fact that practically all authors referred only to classical works such as Cossmann (1904), Cossmann and Pissarro (1906-1913), Deshayes (1824-1837), and Deshayes (1864-1865), who in turn had not seen the type specimen of Lamarck's *Terebellum fusiforme.* It is obvious from the descriptions of those latter authors that they referred to a slender form of "*Terebellum*" occurring in the Cuisian of Cuise-Lamotte. This statement is substantiated by a study of the various old collections housed at different institutions in Paris: all the specimens from Cuise-Lamotte in those collections are labelled *T. fusiforme,* and this form is the only species of Seraphsidae occurring at this locality.

However, *T. fusiforme* of Lamarck needs a new name. This is unfortunate, because *fusiforme* was a widely used name. Favre (1918, explanation of pl. 13, figs. 209a, 209b) was aware of this necessity, who figured and commented upon the type specimen of *Terebellum fusiforme* Lamarck which is deposited in the collections of the Natural History Museum, Geneva. This specimen (see Pl. 3, figs. 4-5), the locality and horizon of which are not known, is an internal cast of *Seraphs sopitus* (Solander, 1766). As mentioned by Favre the original label is missing. And indeed, a comparison of Lamarck's handwriting with that on the label accompanying the specimen shows that they are different.



Text-figure 24. Front view of immature paralectotype of *Seraphs (Diameza) intermedius* from the Lutetian of Grignon near Paris. Ecole des Mines de Paris, Laboratoire de Paléontologie, No. G 2063; 12 ×.

The protoconch of *P. tetanus* (see Pl. 9, fig. 26) is almost planispiral and only slightly elevated over the succeeding whorls. Immature shells are less slender than adult ones. They have a fine sculpture on the lower part of the shell which consists of some spiral grooves with more or less regular interspaces. The shape of the posterior canal of adult specimens is somewhat variable. Usually it reaches the apex only after a bend in an antispiral direction, but rarely it forms a straight line to the apex.

*Measurements (in mm).* — All the measured specimens are from Cuise-Lamotte, the type locality.

| height | diameter | ratio |
|---|---|---|
| 22.4 | 5.6 | 4.0 |
| 23.5 | 6.2 | 3.8 |
| 24.3 | 5.9 | 4.1 |
| 25.0 | 6.7 | 3.7 |
| 25.7 | 6.3 | 4.0 |
| 27.1 | 6.7 | 4.0 |
| 27.2 | 6.8 | 4.0 |
| 28.0 | 7.2 | 3.9 |
| 28.2 | 6.8 | 4.1 |
| 28.3 | 7.3 | 4.0 |
| 28.6 | 7.1 | 4.0 |
| 28.7 | 7.1 | 4.0 |
| 29.6 | 7.4 | 4.0 |
| 29.8 | 7.1 | 4.2 |
| 30.0 | 7.1 | 4.2 |
| 30.0 | 7.4 | 4.1 |
| 31.7 | 7.7 | 4.1 |
| 32.2 | 7.8 | 4.1 |
| 33.7 | 8.2 | 4.1 |
| 34.5 | 8.1 | 4.3 |
| 36.9 | 9.0 | 4.1 |

*P. tetanus* is closely related to *P. placitus* but is more slender than that species and lacks any spiral striation on the whorls. As mentioned under *P. placitus, P. tetanus* appears to be the forerunner of *P. placitus* in the Paris Basin. Differences to other species of *Paraseraphs* are shown in the graph of Text-figure 28.

*Distribution.* — Cuisian (early Eocene), Paris Basin, France. Records of "*Terebellum fusiforme*" from the Eocene of northern Italy either represent other species, or are based on specimens, which cannot be identified with confidence.

### **Paraseraphs armoricensis** (Cossmann)

Plate 9, figures 19-25, Text-figure 28

*Terebellum armoricense* Vasseur, 1880-1917, Faune de Bois-Gouet. Atlas paléontologique. Paris, pl. 2, fig. 20, pl. 3, figs. 55 (late middle Eocene, northwestern France); Cossmann, 1897, Bull. Soc. Sci. Nat. Ouest de la France, vol. 7, fasc. 4, p. 340, pl. 8, figs. 10, 15 (middle Eocene, northwestern France).

*Terebellum armoricum* Vasseur, 1881, Recherches géologiques sur les terrains tertiaires de la France occidentale. Stratigraphie. Première partie: Bretagne. Masson, Paris, pp. 174, 245 (late middle Eocene, northwestern France).

? *Terebellum fusiforme* ? Lamarck, Cailliaud, 1856, Bull. Soc. géol. France, sér. 2, vol. 13, p. 42 (middle Eocene, northwestern France); Vasseur, 1881, Recherches géologiques sur les terrains tertiaires de la France occidentale. Stratigraphie. Première partie: Bretagne. Masson, Paris, p. 232 (middle Eocene, northwestern France).

? *Terebellum cylindricum* Cailliaud, 1856, Bull. Soc. géol. France, sér. 2, vol. 13, p. 42 (*nomen nudum*) (middle Eocene, northwestern France); Vasseur, 1881, Recherches géologiques sur les terrains tertiaires de la France occidentale. Stratigraphie. Première partie: Bretagne. Masson, Paris, p. 232 (middle Eocene, northwestern France).

? *Terebellum* cf. *fusiforme* Lamarck, Cuvillier, 1933, Mém. Inst. Egypte, vol. 22, p. 46, pl. 5, figs. 16, 19 (middle Eocene, Egypt).

? *Terebellum propedistortum* de Gregorio, Oppenheim, 1906, Palaeontographica, vol. 30, 3. Abt., 2. Lief., p. 299 (middle Eocene, Egypt). Cuvillier, 1930, Mém. Inst. Egypte, vol. 16, p. 253 (upper Eocene, Egypt).

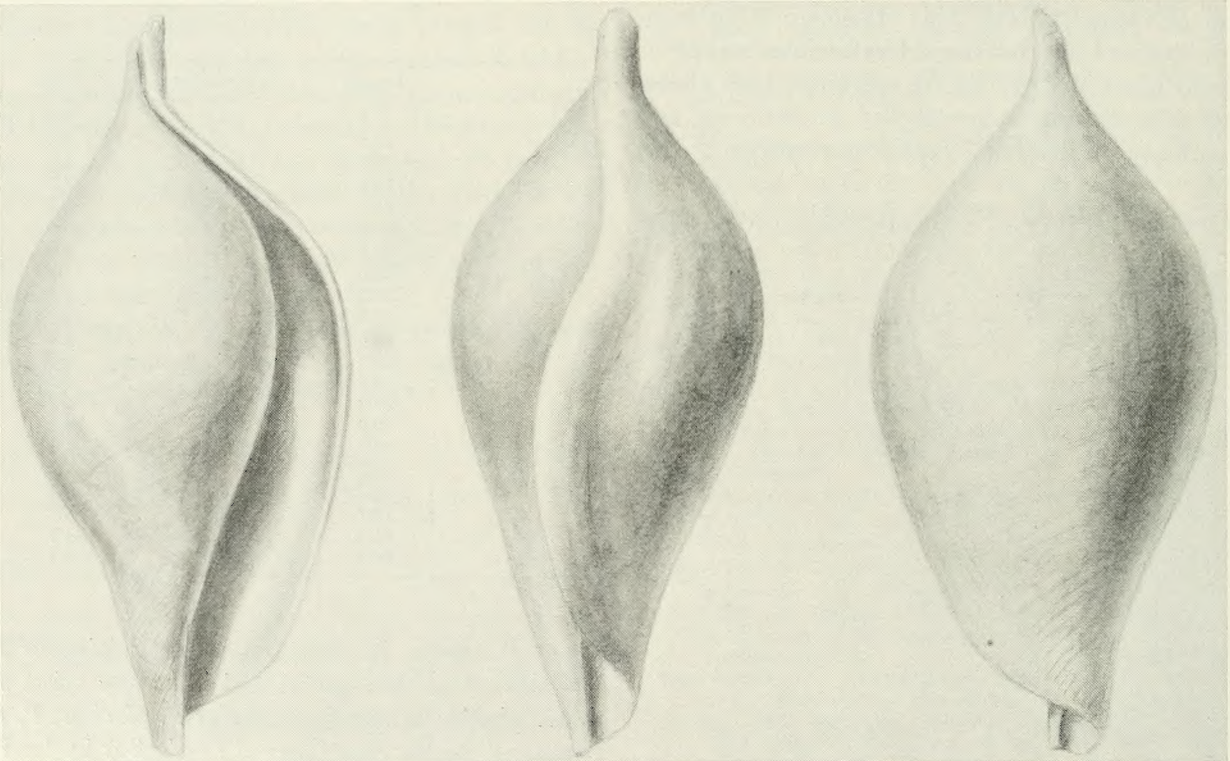
*Description.* — Of large size, slender. Protoconch unknown. Postnuclear whorls about 2½. Surface smooth except for fine growth lines. Callus on inner lip moderately well developed. Outer lip not thickened. Posterior canal runs toward the apex in a slightly antispiral direction. Columella bent backwards near base.

*Holotype.* — Specimen figured by Cossmann (1897, pl. 8, figs. 10, 15) from the Dumas collection (Museum of Nantes ?).

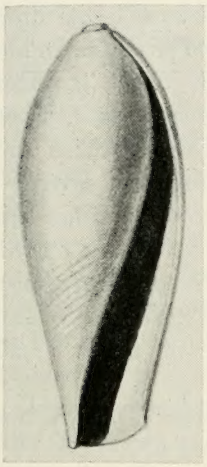
*Dimensions of holotype.* — Height 73 mm; maximum diameter 13 mm.

*Type locality.* — Bois-Gouet, basin of Saffré (Loire-Inférieure), France. Middle Eocene; Biarritzian (late middle Eocene) according to Hottinger and Schaub (1960, p. 468).

The author of this species is Cossmann and not Vas-



Text-figure 25. Three views of *Seraphs (Diameza) intermedius* from the Lutetian of Grignon near Paris. Ecole des Mines de Paris, Laboratoire de Paléontologie, unnumbered. Coll. Caillat; 12 ×.



Text-figure 26. Front view of immature shell of *Paraseraphs tetanus* from the Cuisian of Aizy-Jouy (Aisne), France. Muséum National d'Histoire Naturelle, Paris, no. B 63205. 12 ×.

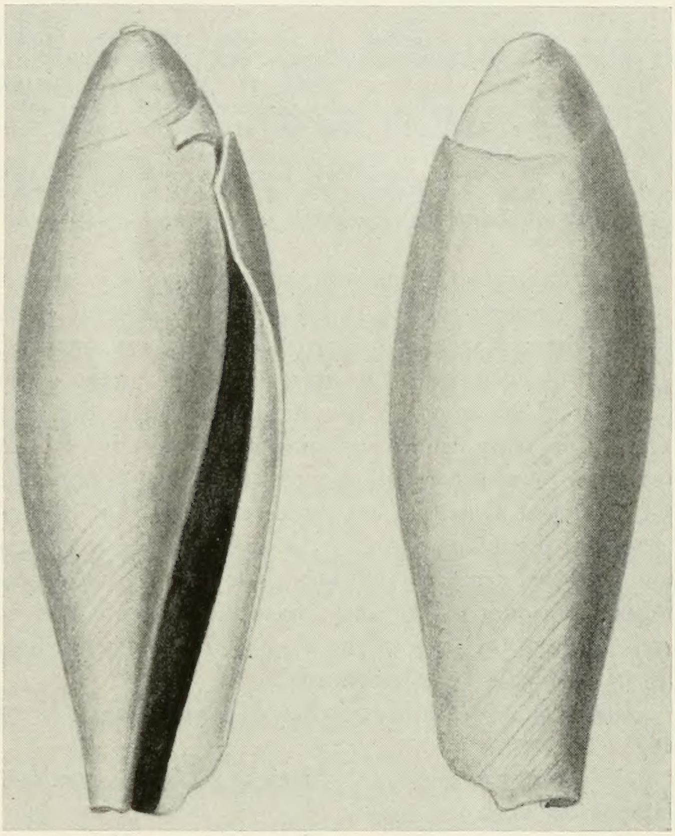
seur, because Vasseur (1881, pp. 174, 245) published the name *armoricum* as a *nomen nudum*. The plates of fossils from Bois-Gouet, which Vasseur prepared, were sent to some of his friends only, *i.e.* they were not generally available, and, therefore, cannot be considered as a publication. These plates were published by Cossmann after Vasseur's death (Vasseur, 1880-1917), but the plates have not been dated individually. The first valid description of the species, therefore, is that by Cossmann (1897).

*Measurements (in mm).* — The first values listed below pertain to a specimen from the early Eocene of Monte Postale, northern Italy; the others to shells from Bois-Gouet, the type locality, which were figured by Vasseur and Cossmann respectively. They are the only complete topotypes known to the writer.

| height | diameter | ratio |
|---|---|---|
| 57.0 | 10.4 | 5.5 |
| 59 | 11.3 | 5.2 |
| 73 | 13 | 5.6 |

*P. armoricensis* is most closely related to *P. tetanus*, from which it can be separated mainly because of its larger size. *P. armoricensis* is usually about twice as high as *P. tetanus*. In addition it is somewhat more slender. *P. propedistortus* is somewhat smaller than *P. armoricensis*, and its spire is more pointed. As mentioned under *P. propedistortus*, which tends to be involute, *P. armoricensis* remains evolute. A relatively well-preserved specimen from the early Eocene of Monte Postale, northern Italy (see Pl. 9, figs. 20-21), identified as *P. armoricensis* is 57 mm high, has a maximum diameter of 10.4 mm, and, therefore, a ratio of 5.5. This ratio compares well with those of topotypes, but not with the ratios of *P. propedistortus*.

*Distribution.* — Early Eocene, northern Italy. Late middle Eocene, northwestern France. Middle Eocene, Egypt (?), Upper Eocene, Egypt (?).



Text-figure 27. Two views of immature *Paraseraphs tetanus* from the Cuisian of Aizy-Jouy (Aisne), France. Muséum National d'Histoire Naturelle, Paris, No. B 63205; 12 ×.

### **Paraseraphs** cf. **armoricensis** (Cossmann)

Plate 11, figures 1-6

This form is known only from eight specimens contained in lot 135097 of the U.S. National Museum, Washington, D.C. They are preserved as internal casts and had been collected near Port Antonio, Portland Parish, Jamaica, from a horizon presumably belonging to the White Limestone. As mentioned under *Seraphs* cf. *sopitus* (Solander) the White Limestone near Port Antonio is of middle or more probably of late Eocene age.

The unsatisfactory state of preservation of these specimens does not allow a definite identification. The largest specimen is almost complete and measures 56.9 mm in height and 11.6 mm in largest diameter. These dimensions, however, are still smaller than those of *P. armoricensis* from the middle Eocene of France, with which it may be compared best.

*Distribution.* — Late (?) Eocene, Jamaica.

### **Paraseraphs placitus**, n. sp.

Plate 10, figures 13-18, Text-figure 28

*Terebellum fusiforme* Lamarck, J. Sowerby, 1821, The Mineral Conchology of Great Britain, vol. 3, p. 157, pl. 287, lower figures (upper Eocene, southern England); Deshayes, 1824-1837, Description des coquilles fossiles des environs de Paris, vol. 2, p. 738, 1837. Atlas, pl. 95, figs. 30, 31 (middle Eocene, Paris Basin).

? *Terebellum (Terebellum) fusiforme* Lamarck, Glibert, 1938, Mém. Mus. Roy. Hist. Nat. Belgique, No. 85, p. 65, pl. 4, fig. 7 [Sables de Wemmel (Bartonian), Belgium].

*Description.* — Of medium size, moderately slender. Protoconch consists of 1¼ to 1½ almost planispiral, glassy whorls. Postnuclear whorls up to 2¼. Sculpture consists of faint growth lines and a fine spiral striation on the uppermost part of the whorl. A few spiral grooves on the lower part of the body whorl adjoining the inner lip are also present on well-preserved specimens. Callus of inner lip well developed. Outer lip not thickened below, but thickening toward the adapical end of the aperture, and continuing as a posterior canal to the apex. The callus of the inner lip also continues to the apex. Base of outer lip does not reach down to the level of the base of the columella. Basal part of columella bent backwards.

*Holotype.* — Naturhistorisches Museum Basel, No. H 14491.

*Dimensions of holotype.* — Height 22.7 mm; maximum diameter 6.3 mm.

*Type locality.* — Chaussy, Dept. Seine-et-Oise, France. Lutetian (middle Eocene).

Most of the specimens studied have been collected from the Lutetian of Chaussy, the type locality. Five specimens at the Ecole des Mines de Paris labelled: Parnes, Mouchy, which had been collected by Deshayes, reach larger dimensions (up to 30 mm in height) than topotypes. But all the other morphological details are identical.

*Measurements (in mm).* — All the measured specimens are from Chaussy, the type locality.

| height | diameter | ratio |
|---|---|---|
| 21.1 | 6.1 | 3.5 |
| 21.8 | 6.2 | 3.5 |
| 22.7 | 6.3 | 3.6 |
| 24.2 | 6.6 | 3.7 |
| 25.0 | 6.5 | 3.8 |
| 25.0 | 6.9 | 3.6 |
| 25.4 | 7.1 | 3.6 |
| 26.8 | 7.2 | 3.7 |
| 26.8 | 7.7 | 3.5 |
| 27.3 | 7.9 | 3.5 |
| 27.5 | 7.6 | 3.6 |
| 27.8 | 7.5 | 3.7 |
| 28.7 | 8.2 | 3.5 |

*P. placitus* is closely related to *P. tetanus* but it differs in being stouter. *P. tetanus* lacks any spiral striation. In most specimens of *P. placitus* the posterior canal is almost straight and runs directly to the apex, whereas in *P. tetanus* it is bent in an antispiral direction. Despite these small differences *P. placitus* is retained as a separate species. In the Paris Basin *P. tetanus* is restricted to the Cuisian being replaced by *P. placitus* in the Lutetian. Specimens recorded from the upper Eocene of England as *Terebellum fusiforme* represent *P. placitus*. Like *P. tetanus P. placitus* is easily distinguished from *P. armoricensis* by its much smaller size.

*Distribution.* — Middle Eocene, Paris Basin, France. Upper Eocene, southern England, Belgium (?).

### **Paraseraphs propedistortus** (de Gregorio)

Plate 11, figures 7-17, Text-figure 28

*Terebellum propedistortum* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi. Palermo, p. 20, pl. 5, figs. 17, 18, 34 (middle Eocene, northern Italy); de Gregorio, 1896, Ann. Géol. Paléont., livraison 21, p. 36, pl. 3, fig. 6 (middle Eocene, northern Italy); Oppenheim, 1896, Palaeontographica, vol. 43, p. 195 (early Eocene, northern Italy); Fabiani, 1915, Mem. Ist. Geol. Padova, vol. 3, p. 255 (middle Eocene, northern Italy); Malaroda, 1954, Mem. Ist. Geol. Min. Univ. Padova, vol. 19, p. 57 (early Eocene, northern Italy).

? *Terebellum propedistortum* de Gregorio, Oppenheim, 1906, Palaeontographica, vol. 30, 3. Abt., 2. Lief., p. 299 (middle Eocene, Egypt); Schlosser, 1925, Abh. Bayer. Akad. Wiss., math.-naturwiss. Abt., vol. 30, No. 7, p. 103 (middle Eocene, Bavaria, Germany); Cuvillier, 1930, Mém. Inst. Egypte, vol. 16, p. 253 ("upper Eocene", Egypt).

? *Limneus clavus* Schafhäutl, 1863, Süd-Bayerns Lethaea Geognostica, p. 212, pl. 47, fig. 16 (middle Eocene, Bavaria, Germany).

*Description.* — Of medium to large size, slender. Spire high and pointed, evolute, but covered by a thin layer of shell material. Outer lip not thickened. Posterior canal almost straight, running in an antispiral direction toward the apex. Due to the thin wash on the spire the canal is not prominent. Anteriormost part of the shell not known.

*Type.* — According to Malaroda (1954, p. 4) De Gregorio's collections were destroyed during the Second World War. However, there are some exceptions as shown by Palmer and Brann (1965, p. 12) for material from the Eocene of Alabama. The type specimen of *Terebellum propedistortum* was not found and turned over to the Paleontological Research Institution. Unfortunately the total material was badly mixed.

*Type locality.* — San Giovanni Ilarione, north of Verona, Italy. Lutetian (middle Eocene).

*P. propedistortus* is characterised by the thin wash on the spire behind the posterior canal. This feature seems to represent an intermediate stage between the genera *Seraphs* and *Paraseraphs*. Although *P. propedistortus* tends to be involute, it is assigned to the genus *Paraseraphs*, mainly on account of its posterior canal, which can be observed on the best specimens available, but also because of its slender, fusiform shape. On the other hand *S. leukoleptus*, n. sp. is considered to be a member of the genus *Seraphs* despite its slender, fusiform shape. That species, however, is entirely involute, which is the most diagnostic feature of *Seraphs*.

It appears, therefore, that *P. propedistortus* and *S. leukoleptus*, n. sp. represent a group which links *Paraseraphs* with *Seraphs* and thus demonstrates their relationship (see also under *S. chilophorus*).

The specimens from the type area of *P. propedistortus* available are not well preserved, and according to the literature there seem to be no satisfactory specimens known. They are either immature or incomplete and usually by far the largest part of the shell material is dissolved. Specimens from the Mokattam area of Egypt cannot be identified with much confidence, because they occur only as internal casts.

*Measurements (in mm).* — Two of the measured specimens have been collected from near the type area of the species.

| height | diameter | ratio |
|---|---|---|
| 41 | 9 | 4.6 |
| 54 | 11.8 | 4.6 |
| 55 (estimated) | 11.9 | 4.6 |

As mentioned above *P. propedistortus* is distinguished from the other species of *Paraseraphs* by the thin wash behind the posterior canal. As far as dimensions and proportions are concerned it approaches *P. armoricensis* (see Text-fig. 28) but remains smaller than that species.

*Distribution.* — Early Eocene, northern Italy. Middle Eocene, northern Italy, Germany (?), Egypt (?). Upper Eocene, Egypt (?).

### **Paraseraphs procerus** (Merian)

Plate 12, figures 1-7, Text-figure 28

*Terebellum procerum* Merian, 1844, Verhandl. Naturf. Ges. Basel, Bd. 6, p. 64 (middle Eocene, Jamaica); Rutsch, 1931, Eclogae geol. Helv., vol. 24, No. 2, p. 254, footnote.

*Terebellum (Terebellum) procerum* Merian, Jung, 1966, Verhandl. Naturf. Ges. Basel, Bd. 77, No. 1, p. 76, Abb. 1-3 (middle Eocene, Jamaica).

? *Terebellum (Terebellum) procerum* Merian ?, Woodring, 1959, U.S. Geol. Sur., Prof. Paper 306-B, p. 192, pl. 25, figs. 5, 7 (late Eocene, Panamá).

*Terebellum subdistortum* Trechmann, 1923, Geol. Mag., vol. 60, No. 710, p. 349, pl. 18, figs. 8, 9 (middle Eocene, Jamaica).

*Description.* — Of large size, slender. Spire high; apex moderately pointed. Number of whorls three to four. Outer and inner lips not preserved. Columella slightly twisted near base.

*Holotype.* — Naturhistorisches Museum Basel, No. H 14374.

*Dimensions of holotype.* — Height 71.8 mm; maximum diameter 16.4 mm.

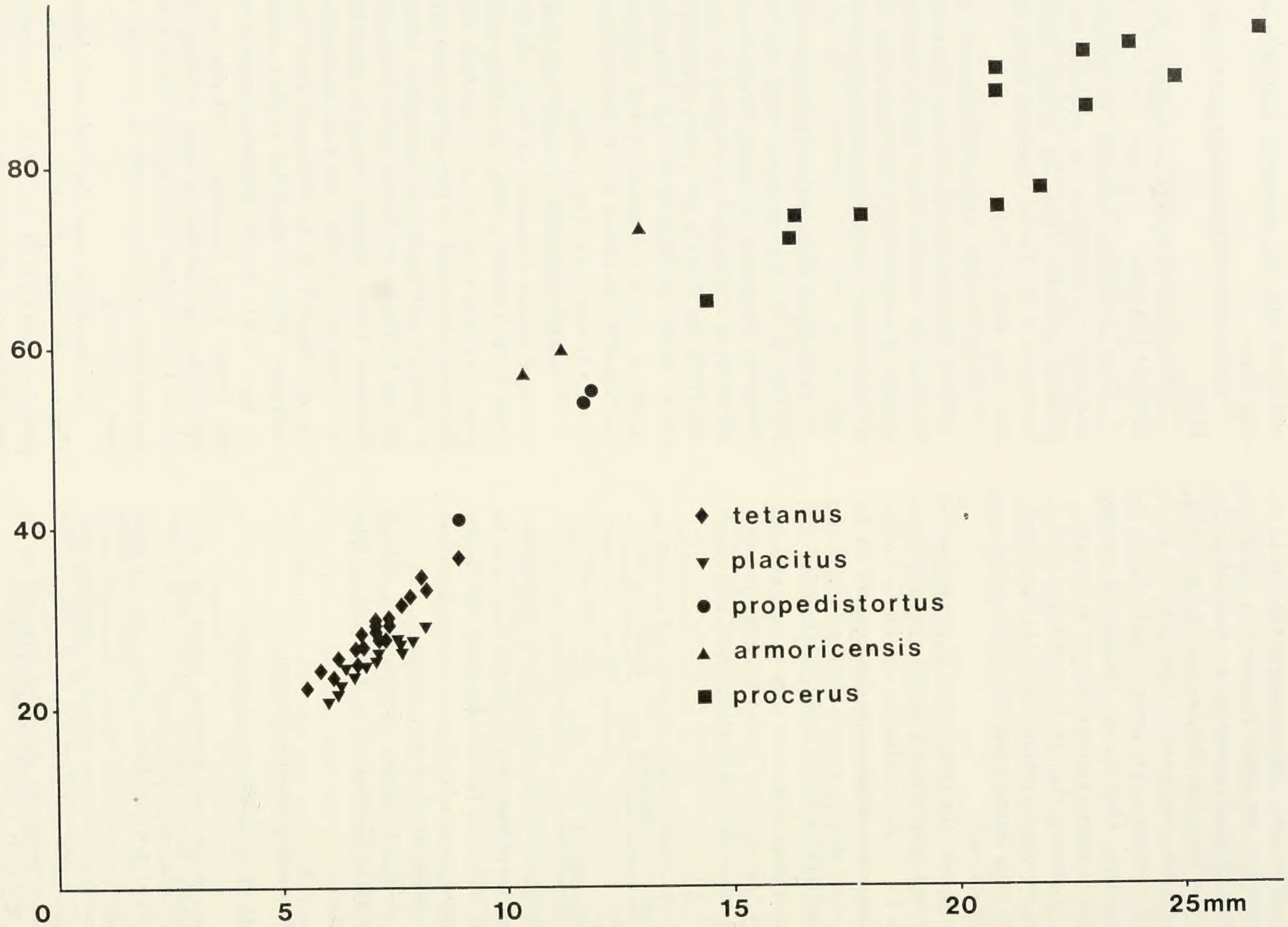
*Type locality.* — Although no precise locality and stratigraphic informations are available, the holotype was probably collected from the middle Eocene Chapelton Formation of the Yellow Limestone Group of Jamaica (see also Jung, 1966, p. 78).

All the available material is preserved as internal casts, and little morphological details can, therefore, be observed. However, the material shows that *P. procerus* is somewhat variable as to apical angle and slenderness. Most specimens are fragmentary, *i.e.* complete steinkerns of *P. procerus* are rare.

*Terebellum subdistortum* Trechmann (1923, p. 349, pl. 18, figs. 8, 9) was described from the middle Eocene Chapelton Formation of Spring Mount, western Jamaica. Its lectotype was selected and figured by Jung (1966) (see also Pl. 12, fig. 7). It is obviously a synonym of *P. procerus*, which occurs abundantly in the Chapelton Formation, mainly in western Jamaica. A few specimens have also been found in the middle to late Eocene Claremont Formation of Claremont, St. Ann, Jamaica.

A single, incomplete internal cast from the middle Eocene Plaisance Limestone of Haiti, which has been collected by E. Lehner in 1934, apparently represents *P. procerus*. Artificial casts of specimens from the late Eocene Gatuncillo Formation of Panamá at hand are identified as *P. procerus* with doubt, and incomplete internal casts from the middle Eocene St. Bartholomew Formation of St. Bartholomew, Lesser Antilles, cannot be identified specifically. An incomplete internal cast from an unspecified Eocene horizon collected on the Maraguán road, 15 miles east of Camaguey, Cuba, is identified as *Paraseraphs* sp. (see Pl. 13, figs. 19-20). Poorly preserved internal casts from the late Eocene Inglis Limestone of Florida, are identified as *Paraseraphs* sp., whereas a large steinkern from the late Eocene Crystal River Formation of Taylor County, Florida, can be identified as *Paraseraphs* cf. *procerus* (Merian) with some confidence.

An incomplete, somewhat deformed, internal cast from Manresa, Barcelona Province, Spain, shows traces of a posterior canal (Pl. 10, figs. 11-12). If complete, the specimen would reach dimensions and proportions which can be compared only with those of *P. procerus*. It is, therefore, identified as *P.* cf. *procerus*. If this identification is cor-



Text-figure 28. Graph showing height/diameter relationships of *P. tetanus*, *P. placitus*, *P. propedistortus*, *P. armoricensis*, and *P. procerus*.

rect, this specimen would extend the geographic range of the species considerably. According to Ferrer (1971, p. 27, table 6) it is highly probable that it had been collected from the Collbás Member of the Santa María Formation which is of late middle Eocene (Biarritzian) age.

*Measurements (in mm).* — The majority of the measurements given below are estimated, because they were taken from incomplete specimens.

| height | diameter | ratio |
|---|---|---|
| 62 | 14.6 | 4.2 |
| 71.8 | 16.4 | 4.4 |
| 74 | 16.5 | 4.5 |
| 74 | 18 | 4.1 |
| 75 | 21 | 3.6 |
| 77 | 22 | 3.5 |
| 86 | 23 | 3.7 |
| 88 | 21 | 4.2 |
| 89 | 25 | 3.6 |
| 90 | 21 | 4.3 |
| 92 | 23 | 4.0 |
| 93 | 24 | 3.9 |
| 94 | 27 | 3.5 |

*P. procerus* is by far the largest species of *Paraseraphs* so far known (see Text-fig. 28). It is considerably larger and less slender than *P. armoricensis* from the middle Eocene of France.

*Distribution.* — Middle Eocene, Jamaica, Haiti. Late Eocene, Panamá (?), Florida (?). Late middle Eocene, Spain (?).

### **Paraseraphs erraticus** (Cooper)

Plate 12, figures 8-14; Plate 13, figures 1-3

*Tornatina erratica* Cooper, 1894, California State Mining Bureau, Bull. 4, p. 47, pl. 2, fig. 35 (Eocene, California); Waring, 1917, California Acad. Sci., Proc., ser. 4, vol. 7, No. 4, p. 91, pl. 15, fig. 11 (upper Eocene, California).

*Terebellum erraticum* (Cooper), Keen and Bentson, 1944, Geol. Soc. America, Spec. Paper No. 56, p. 202.

*Seraphs erratica* (Cooper), Clark, 1926, Univ. Calif. Publ., Bull. Dept. Geol. Sci., vol. 16, No. 5, p. 116 (middle Eocene, California); Clark, *in* Hanna, 1927, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 16, No. 8, p. 260.

*Terebellum californicum* Vokes, 1939, New York Acad. Sci., Ann., vol. 38, pp. 26, 157, pl. 20, figs. 7, 8, 11 (middle Eocene, California); Keen and Bentson, 1944, Geol. Soc. America, Spec. Paper No. 56, p. 199.

*Description.* — Of medium size, moderately slender. Surface smooth. Outer lip not thickened. Exact shape and position of posterior canal not known. Suture indistinct. Columella slightly bent backwards near base.

*Holotype.* — California Academy of Sciences, No. 608.

*Dimensions of holotype.* — Height 19.3 mm; maximum diameter 6.4 mm.

*Type locality.* — Rose Cañon, San Diego County, California. Cretaceous B (= Eocene).

The late Dr. L. G. Hertlein of the California Academy of Sciences kindly sent a photograph and artificial casts of the holotype of *Tornatina erratica* Cooper, which is an incomplete specimen lacking the lower part. I am also indebted to J. H. Peck, Jr. of the Museum of Paleontology, University of California, Berkeley, who sent the type specimens of *Terebellum californicum* Vokes for study. Comparison of this material showed that all the specimens represent one species. The deeply channelled suture of *Tornatina erratica* emphasized by Vokes (1939, p. 157) is due to its state of preservation. The type specimens of *Terebellum californicum* (see Pl. 12, figs. 8-14) have most of the shell material preserved, and their sutures are, therefore, indistinct as expected in species of *Paraseraphs*. The holotype of *T. californicum* clearly shows the lower part of the posterior canal. Its smaller paratype is an immature specimen and the larger paratype is somewhat compressed dorsoventrally.

*P. erraticus* has been cited by Clark (1926, p. 116) from several areas in California. The record of *Terebellum* cf. *californicum* Vokes from the middle Lodo Formation (early Eocene) of the Media Agua Creek area, Kern County, California, given by Mallory (1970, p. 12) should be verified. A single, incomplete, internal cast from the middle Eocene Boca de Serpiente Formation of Soldado Rock, Trinidad (see Pl. 12, figs. 15, 16), is more slender than *P. erraticus,* and its suture is more oblique. It is provisionally identified as *P.* aff. *erraticus.*

*P. erraticus* can be compared with *P. tetanus* from the early Eocene and *P. placitus* from the middle Eocene of the Paris Basin. It differs from both species by its less slender outline and its larger apical angle.

*Distribution.* — Middle and upper (?) Eocene, California.

## Genus **TEREBELLUM** Röding

*Terebellum* Röding, 1798, Museum Boltenianum, Hamburg, pt. 2, p. 135; Lamarck, 1799, Mém. Soc. Hist. Nat. Paris, vol. 1, p. 69, No. 4 (type: *Bulla terebellum* Linné); Montfort, 1810, Conchyliologie systématique, vol. 2, p. 379 (type: *Terebellum subulatum* Lamarck); Blainville, 1825-1827, Manuel de malacologie et de conchyliologie, p. 416, 1825, Atlas, pl. 27, figs. 1, 1a, 1827 (type: *Terebellum subulatum* Lamarck); Winckworth, 1945, Malac. Soc. London, Proc., vol. 26, p. 144 (type by tautonymy: *Terebellum nebulosum* Röding = *Bulla terebellum* Linné, 1767 = *Conus terebellum* Linné, 1758); Jung and Abbott, 1967, Indo-Pacific Mollusca, vol. 1, No. 7, p. 449 (type by indirect tautonymy: *Terebellum nebulosum* Röding = *Conus terebellum* Linné).

*Terebrina* Rafinesque, 1815, Analyse de la Nature, Palermo, p. 145 (emendation for *Terebellum* Lamarck).

*Lucis* Gistel, 1848, Naturgeschichte des Thierreichs für höhere Schulen bearbeitet, Stuttgart, p. 170 (type by monotypy: *L. subulatus*).

*Artopoia* Gistel, 1848, *ibidem,* explanation of pl. 7, fig. 8 (type by monotypy: *A. subulata*).

*Artopoja* Gistel, Paetel, 1887, Catalog der Conchyl.-Samml., Berlin, vol. 1, p. 315.

Type species (by indirect tautonymy and subsequent designation, Winckworth, 1945, Malac. Soc. London, Proc., vol. 26, p. 144): *Terebellum nebulosum* Röding (= *Bulla terebellum* (Linné) = *Conus terebellum* Linné). Recent, western Pacific and Indian Oceans.

*Description.* — Shell slender, cylindrical, evolute, smooth. Suture distinctly channelled. Callus of inner lip prominent and extending as a band just above and along the suture to the apex. Growth lines moderately prosocyrt. Largest diameter of shell near base.

The genus *Terebellum* comprises only four species as compared with *Seraphs* (15 species) and *Paraseraphs* (six species) and is thus the least diversified genus of the family. It is characterised by its slender form and is distinguished from the other genera by its deeply channelled suture.

*Terebellum* always lived in the western Pacific-Indian Oceans area. It did reach the eastern coasts of Africa but never spread into the Mediterranean area and as far as Europe.

*Range.* — Miocene to Recent. The ranges of the species of *Terebellum* are summarized below:

| | early Miocene | middle Miocene | late Miocene | Pliocene | Pleistocene and Recent |
|---|---|---|---|---|---|
| *T. cinctum* | ——— | | | | |
| *T. papilliferum* | ——— | – – —— | – – – – | ——— | |
| *T. obtusum* | | ——— | | | |
| *T. terebellum* | ——— | ——— | ——— | ——— | ——— |

## **Terebellum cinctum** Martin

Plate 13, figures 4-6

*Terebellum (s. str.) cinctum* Martin, 1916, Samml. Geol. Reichs-Museums Leiden, Neue Folge, Bd. 2, Heft 6, p. 248, pl. 2, fig. 53 ("early Miocene", Java).

*Description.* — Of medium size, moderately slender. Spire rather stout. Outer lip not preserved. Callus on inner lip moderately well developed. Suture conspicuous. Above the suture there is a band sculptured by a few fine, spiral threads.

*Holotype.* — Rijksmuseum van Geologie en Mineralogie, Leiden, No. St. 10337.

*Dimensions of holotype.* — Height 34.7 mm; maximum diameter 10.3 mm.

*Type locality.* — Kembang Sokkoh, West Progo Mountains, Java. "Early Miocene".

The holotype of *T. cinctum* is an incomplete, internal cast. The early whorls are deformed. Only small portions of an inner layer of the shell itself are preserved, *e.g.* parts of the callus on the inner lip. The spiral sculpture above the suture of the body whorl is unique. It has not been observed in other species. The shell material of this spirally sculptured area is not preserved in its total thickness. It is possible, therefore, that the original surface was different from that of the specimen as it is preserved now.

This view receives support by a lot collected by Van Dijk from well 4 (depth 130-134 m) in the city of Batavia. This lot (Rijksmuseum van Geologie en Mineralogie Leiden, No. 10350) contains two fragmentary specimens labelled *Terebellum* spec. indet. which were mentioned by Martin twice (1883-1887, p. 312; 1919, p. 125). The age of these specimens was considered as early Pliocene by Martin (1883-1887, pp. 320, 367) and as late Miocene by Martin (1919, p. 125). Three states of preservation can be observed on these specimens: first, the shell material is lacking entirely; second, only an inner layer of the shell is preserved; and third, the shell is preserved in its total thickness. When complete the surface of the shell is smooth. Where an inner layer is preserved the surface is sculptured by spiral striae on areas above the suture, and this sculpture corresponds exactly to that of the holotype of *T. cinctum*. These observations lead to the conclusion that the most diagnostic feature of *T. cinctum* — the spiral sculpture — is not relevant taxonomically and that *T. cinctum*, therefore, should be considered as a *nomen dubium* until better topotypes are available which would allow a clear decision.

The two specimens of the lot mentioned above (No. 10350) probably represent *T. terebellum*. Both are somewhat immature and show the slightly irregular axial sculpture near the apex which is characteristic for the "seraphoid stage" of Recent *T. terebellum* (see Jung and Abbott, 1967, p. 450, pl. 326).

The Rijksmuseum van Geologie en Mineralogie in Leiden has two other specimens (No. 10338) questionably identified by Martin as *T. cinctum*. They were collected from the "early Miocene" of Puntuk tedjo, Res. Djokjakarta, Java. They are preserved as internal casts. The larger one has about the same proportions as the holotype of *T. cinctum*. However, the most diagnostic feature of *T. cinctum*, the spiral sculpture above the suture, is missing.

In general aspect *T. cinctum* seems to be related to *T. papilliferum*. *T. cinctum* is larger and somewhat stouter, but the specimens of both species are not preserved well enough to allow a detailed comparison. In the light of the above considerations, however, it is not excluded that they represent the same species.

*Distribution.* — "Early Miocene", Java.

### **Terebellum papilliferum** Martin

Plate 13, figures 7-11

*Terebellum (s. str.) papilliferum* Martin, 1916, Samml. Geol. Reichs-Museums Leiden, Neue Folge, Bd. 2, Heft 6, p. 248, pl. 2, figs. 51, 52 ("early Miocene", Java).

*Terebellum papilliferum* Martin, Martin, 1928, Mijnbouw in Nederlandsch-Indie, Wetenschappelijke Meded., No. 10, pp. 8, 25 ("Pliocene", Sumatra); Martin, 1928, Leidsche Geol. Meded., deel 3, pp. 108, 109 ("early Miocene", Java).

*Description.* — Of medium size, moderately slender. Spire moderately high, evolute. Surface smooth. Columella almost straight. Suture well marked, bordered by a band of callus which is continuous with the callus of the inner lip. Outer lip slightly thickened.

*Lectotype (herewith selected).* — Rijksmuseum van Geologie en Mineralogie, Leiden, No. St. 10339.

*Dimensions of lectotype.* — Height 28.0 mm; maximum diameter 8.3 mm.

*Type locality.* — Gunung Spolong, West Progo Mountains, Java. "Early Miocene".

The lectotype is the specimen figured by Martin on plate 2, figures 51, 51a. Its outer lip is broken, and its base is not quite complete. The number of visible whorls is a little less than one and a half. The paralectotype figured by Martin on plate 2, figure 52, has a little more than 1½ visible whorls. It is a fragment measuring 18.9 mm in height and 11.2 mm in greatest diameter. Its spire is a little stouter than that of the lectotype which seems to be somewhat immature.

The Rijksmuseum van Geologie en Mineralogie in Leiden has 29 additional specimens of *T. papilliferum.* Twenty-four of them were collected at the type locality, the remainder in the same general area. All the specimens are preserved as internal casts and no morphological details are recognizable.

It is obvious that *T. papilliferum* is related to the Recent *T. terebellum.* In fact it is difficult to separate them. On an average *T. papilliferum* has a somewhat stouter and shorter spire. However, specimens of the Recent *T. terebellum* from Japan and Madagaskar as figured by Jung and Abbott (1967, pl. 321, figs. 9, 10, 12) may have analogous proportions. It is doubtful, whether *T. papilliferum* has any stratigraphic significance. In addition to the "early Miocene" of Java the species has also been reported from the "Pliocene" of Sumatra (Martin, 1928, pp. 8, 25). On the other hand *T. terebellum* is also known from the Pliocene and even from the late Miocene of the Indonesian region. The question, therefore, whether both species should be synonymised or not has to remain unanswered until better material of *T. papilliferum* becomes available.

*Distribution.* — "Early Miocene", Java. "Pliocene", Sumatra.

### **Terebellum obtusum** J. de C. Sowerby

Plate 13, figures 12-18

*Terebellum obtusum* J. de C. Sowerby, *in* Grant, 1840, Geol. Soc. London, Trans., ser. 2, vol. 5, p. 329 and explanation of pl. 26, fig. 31 (middle Miocene, Cutch, India); d'Archiac and Haime, 1854, Description des animaux fossiles du groupe nummulitique de l'Inde, seconde livraison, p. 333, pl. 32, fig. 21 (not fig. 20) (middle Miocene, India).

Not *Terebellum obtusum* Sowerby, d'Archiac, *in* Tchihatcheff, 1850, Bull. Soc. géol. France, sér. 2, vol. 7, p. 405 [= *Seraphs sopitus* (Solander)]; Koch, 1894, Mitt. Jahrb. königl. ungar. geol. Anstalt, vol. 10, pp. 277, 296 [= *Seraphs sopitus* (Solander)]; Doncieux, 1905, Ann. Univ. Lyon, n.s., I. Sci., Méd., fasc. 17, p. 44, pl. 2, fig. 4 [= *Seraphs sopitus* (Solander)].

*Terebellum subulatum* Lamk., var. *obtusum* J. de C. Sowerby, Vredenburg, 1925, Mem. Geol. Survey India, vol. 50, pt. 1, p. 322 (middle Miocene, northwestern India).

*Description.* — Of medium size; moderately slender. Apex not pointed. The spire is relatively short and consists of about 2½ whorls. Suture not prominent. Callus of inner lip well developed. Columella slightly recurved near base.

*Holotype.* — British Museum (Natural History), Dept. of Palaeontology, No. GG 21000.

*Dimensions of holotype.* — Height 42.2 mm; maximum diameter 13.5 mm.

*Type locality.* — Soomrow, Cutch, India. Gaj beds (middle Miocene).

So far *T. obtusum* has been recorded only from the Gaj beds of northwestern India which are of middle Miocene age according to Eames (1970, p. 38). The holotype of this species (see Pl. 13, figs. 17-18) is incomplete and has only parts of the original shell material preserved. The holotype as well as the figured topotype (see Pl. 13, figs. 15-16) are somewhat compressed dorsoventrally. The third specimen of *T. obtusum* available is that figured by d'Archiac and Haime (1854, Pl. 32, fig. 21) from the middle Miocene Gaj beds of Sind (see Pl. 13, figs. 12-14). It is an incomplete specimen showing only the spire and part of the body whorl. The other specimen figured by d'Archiac and Haime (1854, pl. 32, fig. 20) as *T. obtusum* is an internal cast of *Seraphs sopitus* (Solander) (see Pl. 4, figs. 12-13).

A specimen in the Muséum National d'Histoire Naturelle Paris (No. B 22386) from an unspecified Paleogene horizon (probably Eocene) of Zafranboli, Asia Minor, had been studied by d'Archiac (*in* Tchihatcheff, 1850, p.

405) and is labelled *T. obtusum.* This specimen is an internal cast of *Seraphs sopitus* (Solander).

As pointed out by Vredenburg (1925, p. 322) *T. obtusum* is obviously closely related to *T. terebellum,* as is also *T. papilliferum* Martin. However, due to the unsatisfactory state of preservation of the available material of *T. obtusum* a useful comparison with *T. terebellum* is practically impossible. Both species show some variability as to the height of their spire.

*Distribution.* — Middle Miocene, northwestern India.

### **Terebellum terebellum** (Linné)

Plate 14, figures 1-8, Text-figure 13

*Conus terebellum* Linné, 1758, Systema Naturae, ed. 10, p. 718, No. 284 (in Asia).

*Terebellum terebellum* (Linné), Jung and Abbott, 1967. Indo-Pacific Mollusca, vol. 1, No. 7, pp. 445-454, pls. 318-327. For further citations see this publication.

*Lectotype.* — The specimen from the Linnean collection at present at the British Museum (Natural History) marked with the remnants of the number '388'. No locality information (see Pl. 14, fig. 1).

*Dimensions of lectotype.* — Height 37.5 mm; maximum diameter 10.6 mm.

This species has been dealt with by Jung and Abbott (1967). Since then no additional information has become available except for a new record in the Persian Gulf (Biggs, 1973, p. 364).

As mentioned below Wissema (1947, p. 92) recorded *T. terebellum* from the "Plio-Pleistocene" of Nias off the west coast of Sumatra. Earlier Woodward (1879, p. 497, pl. 13, fig. 6) described and figured an internal cast from an unspecified "Tertiary" horizon of Nias, which he identified as *Terebellum* sp. This specimen is refigured here (Pl. 14, figs. 9-11).

*Distribution.* — *T. terebellum* ranges from Miocene to Recent. Living representatives occur from East Africa to Samoa, and from Japan to Australia. Fossil records: Early Miocene: Saipan (Mariana Islands) (Ladd, 1972, p. 57); Miocene: Java (Martin, 1928, p. 25); Quilon, Kerala, India (Dey, 1962, p. 67). Neogene: Java (Oostingh, 1935, p. 59); Saonek besar near New Guinea (Boettger, 1908, p. 674; Oostingh, 1935, p. 59). Pliocene: Java (Oostingh, 1935, p. 59, and others); Sumatra (Martin, 1928, p. 8); North Borneo, Dent Peninsula (Cox, 1948, p. 31; Nuttall, 1965, p. 170); Borneo, North Kutei (collections of the Natural History Museum Basel); Timor (Cox, 1948, p. 31); East Ceram (collections of the Natural History Museum Basel). Plio-Pleistocene: Island of Nias off the west coast of Sumatra (Wissema, 1947, p. 92). Quaternary: Farsan Kebir, Red Sea (Cox, 1931a, p. 7); Dar es Salaam, Tanganyika (Koert and Tornau, 1910, p. 10); Belitung (Billiton) Island east of Sumatra (Martin, 1880, p. 19); Bunju Island, East Borneo (Beets, 1950, p. 244).

## APPENDIX 1

### A. SPECIES ERRONEOUSLY REFERRED TO TEREBELLUM.

The species listed below obviously do not belong to the family Seraphsidae:

### **Terebellum diversiornatum** Eames

Plate 14, figures 12-14

*'Terebellum' diversiornatum* Eames, 1952, Philos. Trans. Royal Soc. London, ser. B, No. 631, vol. 236, p. 74, pl. 3, fig. 77.

*Holotype.* — British Museum (Natural History), Dept. of Palaeontology, No. G 68239.

*Dimensions of holotype.* — Height 10.1 mm; maximum diameter 4.5 mm.

*Type locality.* — Zinda Pir section, Western Punjab, Pakistan. Ghazij shales (lower Eocene).

This species is known from the holotype only which is a small, incomplete, internal cast of a probably immature specimen. The original illustration is an inaccurate drawing, and the holotype is, therefore, refigured here (Pl. 14, figs. 12-14). The affinities of this species are not known.

### **Terebellum schweinfurthi** Oppenheim

*Terebellum schweinfurthi* Oppenheim, 1906, Palaeontographica, vol. 30, 3. Abt., 2. Lief., p. 298, pl. 25, fig. 14; Cuvillier, 1930, Mém. Inst. Egypte, vol. 16, p. 79.

*Holotype.* — Said to be deposited in Berlin.

*Dimensions of holotype.* — Height 20 mm; maximum diameter 8 mm.

*Type locality.* — Schech Mejach, south of Gebel Selseleh, Egypt. Lower Eocene.

This species was also based on a single specimen which is a small, internal cast with uncertain affinities.

### **Seraphs** (?) **thompsoni** Dickerson

*Seraphs (?) thompsoni* Dickerson, 1914, Univ. California Publ., Bull. Dept. Geol., vol. 8, No. 6, p. 144, pl. 14, figs. 6a, 6b; Keen and Bentson, 1944, Geol. Soc. America, Spec. Paper No. 56, p. 192.

*Syntypes.* — University of California, Museum of Paleontology, Berkeley, Nos. 11854, 11855.

*Type locality.* — Univ. Calif. locality 784: vicinity of Lower Lake, Lake County, California. NW ¼ of NE ¼ of Sec. 11, T. 12 N, R. 7 W, about ¼ to ½ mile east and a little south of Lower Lake on Knoxville road, 1000 feet (horizontal distance) above the Chico-Martinez contact, well at old brick yard. Martinez Group, Paleocene.

Due to the kindness of Mr. J. H. Peck, Jr. of the Museum of Paleontology, University of California, Berkeley, I was able to study the two syntypes of this species. They are imperfectly preserved specimens which do not represent a species of the Seraphsidae. As stated by Vokes (1939, p. 157) they probably also do not belong to the Strombidae.

In addition to the three species mentioned above there are four more species names which had been assigned to *Terebellum* by Tuomey and Holmes ("Fossils of South Carolina, Pliocene and Post-Pliocene", pp. 120-122, pl. 26, figs. 7-11, 1855-1860). They are: *T. striatum* Tuomey and Holmes, *T. exaltatum* Conrad, *T. etiwanensis* Tuomey and Holmes, and *T. burdenii* Tuomey and Holmes. All these forms are species of *Turritella* (see also Harris, 1890, p. 315).

B. SPECIES INCERTAE SEDIS.

#### **Terebellum brongniartianum** d'Orbigny

*Terebellum brongniartianum* d'Orbigny, 1850-1852, Prodrome de paléontologie . . ., vol. 2, p. 314, 1850 (middle Eocene, northern Italy).

This species was described casually under the heading *Terebellum brongniartianum*, d'Orb., 1847, but the actual date of publication of this name is 1850 according to Sherborn (Index animalium, p. 899, 1924). D'Orbigny based the name on material from the middle Eocene of Roncá, northern Italy. The species has never been figured nor has it been redescribed or referred to, and nothing is known on the whereabouts of the type material. D'Orbigny merely compared his species with *T. convolutum*.

Under these circumstances it is proposed to consider *T. brongniartianum* as a *nomen dubium*.

#### **Terebellum convofusiforme** de Gregorio

*Terebellum convofusiforme* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi. Palermo, p. 22, pl. 5, fig. 32 (middle Eocene, northern Italy).

De Gregorio stated that he based this name on a small number of badly preserved specimens from the middle Eocene of San Giovanni Ilarione, northern Italy. The specimen De Gregorio figured is an incomplete internal cast which has probably been destroyed (Malaroda, 1954, p. 4). *T. convofusiforme* should be treated as a *nomen dubium*.

#### **Terebellum dautzenbergi** Cuvillier

*Terebellum dautzenbergi* Cuvillier, 1933, Mém. Inst. Egypte, vol. 22, p. 46, pl. 6, figs. 3, 4 (middle Eocene, Egypt).

The figured specimen of this species is a small (height 24 mm) internal cast from the Lutetian of Gebel Mokattam near Cairo, Egypt, the affinities of which are difficult to determine. It might possibly represent the internal cast of a species similar to or identical with *Seraphs olivaceus* from the Lutetian of the Paris Basin, but this is a mere speculation. It seems best to consider *T. dautzenbergi* as a *nomen dubium*, although the figured specimen might be found in Cuvillier's collection at the Sorbonne in Paris.

#### **Terebellum postconicum** de Gregorio

*Terebellum postconicum* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi. Palermo, p. 21, pl. 1, fig. 18 (middle Eocene, northern Italy).

The figured specimen of this species is an incomplete, internal cast with uncertain affinities from the middle Eocene of northern Italy. Only the spire and part of the body whorl are preserved. According to Malaroda (1954, p. 4) the type material is probably destroyed. For these reasons *T. postconicum* should be treated as a *nomen dubium*. Cossmann (1889, p. 96) considered *T. postconicum* as a synonym of *T. fusiforme*.

#### **Terebellum (Seraphs) pisciforme** Martin

*Terebellum (Seraphs) pisciforme* Martin, 1931, Wetenschappelijke Meded., No. 18, p. 37, pl. 5, fig. 11 (late Eocene, Java).

Martin had a single, incomplete specimen measuring 16 mm in height at hand, when he described this species. It had been collected from late Eocene deposits at Kali Puru, Java. The species had never been redescribed nor refigured, and there are no specimens in the collections of the Rijksmuseum van Geologie en Mineralogie in Leiden, where most of the material Martin described is deposited. *T. pisciforme* should, therefore, be treated as a *nomen dubium* until better topotypes become available.

The original figure of *T. pisciforme* suggests that this form may actually represent a species of *Seraphs*. More complete topotypes might eventually show that it is related to slender, cylindrical species of *Seraphs* such as *S. leukoleptus* or *S. belemnitus*.

## APPENDIX 2:

## TEREBELLOPSIS AND SEMITEREBELLUM

*Terebellopsis* Leymerie and *Semiterebellum* Cossmann are not considered to be members of the family Seraphsidae. Following Wenz (Handbuch der Paläozoologie, vol. 6, 1940, Gastropoda, p. 937) they are treated as subgenera of *Tibia* Röding, 1798. *Tibia s. str.* (type species: *Murex fusus* Linné. Recent, Indo-Pacific) is characterised by its high spire, its axially sculptured early whorls, by the possession of a more or less developed rostrum, a digitate outer lip, and a short posterior canal which does not ascend high up the spire.

The systematic position of *Terebellopsis* as defined by Leymerie (1846, p. 365) is difficult to judge. The much better preserved material published by Doncieux (1908, pp. 101-103) allows a clearer understanding of the affinities of *Terebellopsis*. Like *Tibia s. str. Terebellopsis* has a high spire and axially sculptured early whorls. It differs from *Tibia s. str.* in having a long posterior canal which extends up the spire to the apex, and the lack of a rostrum. The outer lip of *Terebellopsis* is not flaring nor digitate.

*Semiterebellum* has also a high spire, but in contrast to *Tibia s. str.* and *Terebellopsis*, it lacks axial sculpture on early whorls. Like *Tibia s. str.* it has a rostrum, but its posterior canal is long as in *Terebellopsis*.

The diagnostic features of *Tibia s. str.*, *Terebellopsis*, and *Semiterebellum* may be summarized as follows:

| | *Tibia s. str.* | *Terebellopsis* | *Semiterebellum* |
|---|---|---|---|
| spire | high | high | high |
| early whorls | axially sculptured | axially sculptured | not axially sculptured |
| outer lip | digitate<br>flaring | not digitate<br>not flaring | flaring |
| posterior canal | short | long | long |
| rostrum | present | absent | present |

*Semiterebellum* was proposed by Cossmann (1889, p. 95) as a section of the genus *Gladius* (= *Tibia*). Cossmann designated *Rostellaria marceauxi* Deshayes (1864-1865, p. 462, pl. 88, figs. 16, 17, 1865) from the Thanetian (Paleocene) of Jonchery-sur-Vesle, Dept. Marne, France, as the type species of his new section. A topotype of *T. marceauxi* is here figured (Pl. 15, figs. 13-15). The whorls of *T. marceauxi* are sculptured by spiral grooves, the posterior canal extends almost up to the apex, and its outer lip is somewhat flaring. The rostrum of the figured specimen is missing.

*Terebellopsis leymeriei* Villatte (1962, p. 211, pl. 10, figs. 7-9) from the "Montian" of southern France is probably a species of *Semiterebellum*. Villatte's figure 8 on plate 10 shows a specimen which has a flaring outer lip like *T. marceauxi*. The age of the beds, from which *T. leymeriei* was collected, is now considered to be early Thanetian (Tambareau and Villatte, 1968 p. 58).

*Rostellaria postalensis* Bayan (1870a, p. 480; 1870b, p. 47, pl. 2, figs. 1, 2; Oppenheim, 1896, p. 193, pl. 17, figs. 2, 3) from the early Eocene of Monte Postale, northern Italy, and its subspecies from the same locality and horizon, have been assigned to the subgenus *Semiterebellum* by Malaroda (1954, pp. 56-57) and Malaroda (1960, p. 221). All these forms have a rather short spire with a large apical angle; they have a short posterior canal and lack a rostrum. They certainly do not belong to *Semiterebellum* and need reclassification.

Newton (1922) described two species from the middle or upper Eocene of Bende Ameki, Nigeria, which he referred to *Semiterebellum*: *S. suturocostatum* Newton (1922, p. 15, pl. 4, figs. 14-17) and *S. elongatum* Newton (1922, p. 17, pl. 2, figs. 14, 15). Both lack a rostrum, their posterior canal is short, and, therefore, they do not belong to *Semiterebellum*. Eames (1957), who was aware of this, reclassified both of Newton's species generically. He proposed *Africoterebellum* as a subgenus of *Semiterebellum* (Eames, 1957, p. 37) with *S. elongatum* Newton as its type species, and *S. suturocostatum* served as type species for his new genus *Amekichilus* (Eames, 1957, p. 38). He considered *Amekichilus* to be related to *Ectinochilus* and *Dientomochilus*.

Some material originally assigned to *Terebellum* by previous workers should actually be referred to *Terebellopsis*. Some of its species are, therefore, treated in some detail.

### Subgenus **TEREBELLOPSIS** Leymerie

*Terebellopsis* Leymerie, 1846, Mém. Soc. géol. France, sér. 2, vol. 1, pt. 2, p. 365.

Type species (by monotypy): *Terebellopsis brauni* Leymerie. Paleocene, southern France.

The diagnostic features of *Terebellopsis* are summarized above and its systematic position as a subgenus of *Tibia* mentioned.

*Range.* — Late Paleocene to middle Eocene.

### **Tibia (Terebellopsis) brauni** Leymerie

Plate 15, figures 1-3

*Terebellopsis brauni* Leymerie, 1846, Mém. Soc. géol. France, sér. 2, vol. 1, pt. 2, p. 365, pl. 16, fig. 8 [Ilerdian (late Paleocene), France]; Gabrielian, 1964, Paleogene and Neogene of the Armenian SSR (in Russian). Yerevan; p. 73 ("middle Eocene", Armenia).

*Terebellopsis brauni* (Leymerie), Plaziat and de Renzi, 1968, Mém. Bureau Rech. Géol. Min., No. 58, p. 578 ["middle Eocene" = Ilerdian (late Paleocene), southern France].

*Rostellaria (Terebellopsis) brauni* Leymerie, Doncieux, 1908, Ann. Univ. Lyon, n.s., I. Sci., Méd., fasc. 22, p. 102, pl. 5, figs. 7a, 7b ["middle Eocene" = Ilerdian (late Paleocene), southern France].

*Terebellum braunii* Leymerie, d'Orbigny, 1850-1852, Prodrome de paléontologie . . ., vol. 2, p. 314, 1850.
*Terebellum brauni* Leymerie, Doncieux, 1905, Ann. Univ. Lyon, n.s., I. Sci., Méd., fasc. 17, p. 45, pl. 2, fig. 1 [Ilerdian (late Paleocene), southern France].
? *Terebellopsis brauni* Leymerie, Bellardi, 1852, Mém. Soc. géol. France, sér. 2, vol. 4, pt. 2, pp. 217, 291 (middle Eocene, southeastern France). Fabiani, 1915, Mem. Ist. Geol. Univ. Padova, vol. 3, Mem. 1, p. 255 ("middle Eocene", nothern Italy).
? *Terebellum distortum* d'Archiac and Haime, Cossmann and Pissarro, 1909, Palaeont. Indica, new ser., vol. 3, memoir 1, p. 49, pl. 5, figs. 6, 7, not fig. 11 (= *Paraseraphs* sp.) (late Paleocene, Sind).

*Syntypes.* — Coll. Leymerie, Muséum d'Histoire Naturelle, Toulouse, France.

*Type locality.* — Leymerie recorded this species from three localities of the Montagne Noire area: Montolieu, Conques, and Villegalhène. Montolieu is herewith selected as the type locality. Age: Ilerdian (late Paleocene).

Leymerie based *T. brauni* on high-spired, internal casts, which are said to be most abundant at certain localities. The specimen from the type locality here figured (Pl. 15, figs. 1-3) belongs to the Leymerie collection, which is housed at the Natural History Museum of Toulouse. It possibly represents a syntype. No specimens of *T. brauni* were known which had their shell or parts of their shell preserved until Doncieux (1908, pl. 5, figs. 7a, 7b) figured a specimen from the "middle Lutetian" (= Ilerdian: late Paleocene) of Coustouge, southern France. This specimen shows that the first five whorls are sculptured by axial costae and that the subsequent whorls are smooth. The posterior canal is slightly curved on that specimen and extends up to the apex. Its outer lip is not flaring, and there is no sign of a rostrum. Doncieux's material was actually the base for the extended definition of *Terebellopsis*.

Another species of *Terebellopsis* occurring at the same level as *T. brauni* and obviously closely related to it is *T. rabetensis* Doncieux (1908, p. 103, pl. 5, figs. 8a, 8b). At its type locality it occurs together with *T. brauni*. It is smaller than *T. brauni* and appears to have a somewhat irregular spire. As pointed out by Doncieux the two species also differ in details of the axial sculpture on their early whorls.

As mentioned above *T. leymeriei* (Villatte) (1962, p. 211, pl. 10, figs. 7-9) from the "Montian" (early Thanetian according to Tambareau and Villatte, 1968, p. 58) of southern France was originally assigned to *Terebellopsis*, but it probably represents a species of *Semiterebellum* on account of its flaring outer lip.

Under the name of *Terebellum distortum* Cossmann and Pissarro (1909, p. 49) figured high-spired specimens (pl. 5, figs. 6-7; not fig. 11) from the late Paleocene Upper Ranikot beds, which Vredenburg (1928, pp. 47, 49) reidentified as *T. lanceolata* (Cossmann and Pissarro) (1909, p. 50, pl. 5, fig. 8). These internal casts do not show any indication of a flaring outer lip, and should be assigned to *Terebellopsis* rather than to *Semiterebellum* as suggested by Vredenburg. Cossmann and Pissarro's figure 11 on plate 5 has been reversed during the process of reproduction (Vredenburg, 1928, p. 49, footnote). According to the type of winding (the sutures becoming more and more oblique with increasing age) and the traces of a posterior canal this specimen most likely represents a species of *Paraseraphs*.

A moderately well-preserved specimen contained in the collections of the U.S. National Museum (see Pl. 14, figs. 15-16) is accompanied by the following label: "Jhirak, Sind. Nummulitique". It is highly probable that the specimen was collected from the upper Ranikot beds of Jhirak, which are of late Paleocene age according to Nagappa (1959, p. 150) and Adams (1970, fig. 2). The specimen clearly shows a posterior canal, but the outer lip and part of the body whorl are missing. It is identified as *Paraseraphs* ? sp. If this specimen and the one figured by Cossmann and Pissarro (1909, pl. 5, fig. 11) really represent species of *Paraseraphs,* Text-figure 10 would have to be modified. However, to reach a conclusion, more and better material is needed.

A single, internal cast from Simpheropol, Crimea, contained in the collection of Mayer-Eymar is identified as *T.* cf. *brauni* (see Pl. 15, figs. 4-6). The age of the beds from which it was collected is indicated as Parisian I (= Lutetian) by Mayer-Eymar, but it is possible that these beds are actually older. The specimen has no flaring outer lip, but shows traces of a posterior canal ascending the spire to the apex.

*Terebellum (Seraphs) lanceolatum* Cossmann and Pissarro (1909, p. 50, pl. 5, fig. 8) was based on a badly preserved specimen from the Upper Ranikot beds (late Paleocene) of Jhirak, Sind. It may well represent a species of *Semiterebellum* as suggested by Vredenburg (1925, p. 323; 1928, p. 47) or of *Terebellopsis.* However, the species is not known well enough and should be considered as a *nomen dubium* until better material becomes available.

*Rostellaria bellardii* de Gregorio (1880, p. 18, pl. 5, figs. 14a, 14b) from the Lutetian (middle Eocene) of San Giovanni Ilarione, northern Italy, is a large and massive species which is assigned to the subgenus *Terebellopsis.*

*Distribution.* — Late Paleocene, southern France. Younger occurrences mentioned in the literature need confirmation.

### **Tibia ? (Terebellopsis ?) distorta** (d'Archiac and Haime)

Plate 15, figs. 7-12

*Terebellum distortum* d'Archiac and Haime, 1854, Description des animaux fossiles du groupe nummulitique de l'Inde. Seconde livr., p. 334, pl. 32, figs. 19, 19a (late Paleocene, Pakistan); Vredenburg, 1928, Palaeont. Indica, new ser., vol. 10, mem. 4, p. 49 (late Paleocene, Pakistan).

? *Terebellum* sp., Doncieux, 1905, Ann. Univ. Lyon, new ser., I. Sci., Méd., fasc. 17, p. 46, pl. 2, fig. 5 (late Paleocene, southern France).

Not *Terebellum distortum* d'Archiac and Haime, Cossmann and Pissarro, 1909, Palaeont. Indica, new ser., vol. 3, mem. 1, p. 49, pl. 5, figs. 6, 7, not fig. 11 (= *Paraseraphs* sp. ind.) (late Paleocene, Pakistan); Douvillé, 1916, Palaeont. Indica, new ser., vol. 5, mem. 3, p. 21, pl. 7, figs. 8a, 8b (Danian, Tibet: Paleocene according to Nagappa, 1959, p. 162).

Not *Terebellum (Seraphs) distortum* d'Archiac, Tessier, 1952, Contributions à la stratigraphie et à la paléontologie de la partie ouest du Sénégal (Crétacé et Tertiaire), Dakar, vol. 2, p. 374, pl. 32, figs. 14, 15 (early Eocene, Senegal).

Not *Terebellum (Terebellum) distortum* d'Archiac and Haime, Bagmanov, 1966, Larger Foraminifera and mollusk fauna of the Eocene deposits of the Trans-Caucasus (Russian). Baku, p. 179, pl. 81, figs. 7-10 (middle Eocene, Trans-Caucasus).

*Syntypes.* — British Museum (Natural History), Dept. of Palaeontology, Nos. GG 21005 and GG 21006.

*Dimensions of syntypes.* — GG 21005: height 41.2 mm, maximum diameter 13.0 mm. GG 21006: height 37.9 mm, maximum diameter 13.3 mm.

*Type locality.* — Ranikot, Sind, Pakistan. Late Paleocene.

*T. distorta* was based on the two syntypes here figured, which are internal casts of unsatisfactory preservation. Syntype GG 21005 corresponds to d'Archiac and Haime's figure 19, and syntype GG 21006 to figure 19a on plate 32. The spire of these specimens is not distorted as the name might imply. Judging from their general shape it is possible that they represent a species of *Terebellopsis*, although no traces of a posterior canal are preserved. But the species is not known well enough and is, therefore, considered as a *nomen dubium*.

From a study of the literature one gets the impression that this species served as a welcome harbour for badly preserved material. Evidence for this statement is provided by Douvillé (1916, p. 21, pl. 7, figs. 8a, 8b), Tessier (1952, p. 374, pl. 32, figs. 14, 15), and Bagmanov (1966, p. 179, pl. 81, figs. 7-10).

## APPENDIX 3: MAURYNA

### Genus **MAURYNA** de Gregorio

*Mauryna* de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1: Cefalopodi e Gasteropodi. Palermo, p. 24; Wenz, 1938-44, Handbuch der Paläozoologie. Borntrager, Berlin, vol. 6, pt. 4, p. 939.

Type species (by subsequent designation, Cossmann, 1904, Essais de paléoconchologie comparée, livraison 6, p. 46): *Terebellum plicatum* d'Archiac and Haime. Late Paleocene, Pakistan.

*Description.* — Of medium to large size, moderately slender, evolute. Spire consists of about three whorls. Suture indistinct. Whorls sculptured by axial costae, which are narrow on spire whorls, but become much coarser and distant on the last portion of the body whorl. Inner lip thin; outer lip somewhat thickened. The posterior canal extends from the adapical end of the aperture to the apex and continues on the opposite side as far down as the upper part of the body whorl. Columella apparently not twisted near base.

*Range.* — Late Paleocene, Pakistan.

De Gregorio (1880, p. 24) introduced the name *Mauryna* as a subgenus of *Terebellum* for species with axial sculpture. He did not designate a type species but listed as examples *M. plicata, M. protoelegans,* and *M. plicifera.* As indicated above Cossmann (1904, p. 46) subsequently designated *Terebellum plicatum* as the type species of *Mauryna.*

With the possible exception of *M. costata* (Martin) (1931, p. 38, pl. 5, figs. 12, 12a) from the Upper Eocene of Java (see below) *M. plicata* (d'Archiac and Haime) is the only species of the genus. The species from the middle Eocene of northern Italy assigned to *Mauryna* by De Gregorio (1880, p. 24) belong to the genus *Seraphs* (see discussion under *Seraphs plicifer*); although they have axial swellings, their sculpture remains much weaker than that of *M. plicata.* In addition they are all involute and lack the characteristic canal of *M. plicata.*

The genus *Mauryna* is here excluded from the Seraphsidae mainly because of its strong, axial sculpture. Despite its canal, which is somewhat similar to that of certain species of *Paraseraphs, Mauryna* appears to be more closely related to the genera *Rimella* and *Ectinochilus,* although it reaches larger dimensions.

### **Mauryna plicata** (d'Archiac and Haime)

Plate 16, figures 1-14

*Terebellum plicatum* d'Archiac and Haime, 1854, Description des animaux fossiles du groupe nummulitique de l'Inde, seconde livraison, p. 334, pl. 32, figs. 17, 18 (not fig. 22 = *Seraphs sopitus* (Solander) ?) ("Eocene", Pakistan).

*Mauryna plicata* d'Archiac, de Gregorio, 1880, Fauna di S. Giovanni Ilarione (Parisiano). Parte 1. Cefalopodi e Gasteropodi. Palermo, p. 24.

*Terebellum (Mauryna) plicatum* d'Archiac and Haime, Cossmann and Pissarro, 1909, Palaeont. Indica, new ser., vol. 3, No. 1, p. 50, pl. 5, figs. 3, 4, 5 (late Paleocene, Pakistan); Vredenburg, 1928, Palaeont. Indica, new ser., vol. 10, mem. 4, p. 50 (late Paleocene, Pakistan).

*Description.* — Of medium to large size, moderately slender. Spire moderately high. Apex not pointed. Spire consists of about three whorls. Suture indistinct. Sculpture consists of axial costae, which are weak and closely spaced on early whorls, but which gradually become stronger and more widely spaced on late whorls. On the last portion of the body whorl they are prominent and have wide interspaces. Inner lip thin. Outer lip slightly thickened on upper part. The posterior canal extends from the adapical end of the aperture to the apex and on the opposite side down to the upper portion of the body whorl. From an apical view this canal lies practically in one plane. Columella apparently not twisted near base.

*Lectotype (herewith selected).* — British Museum (Natural History), Dept. of Palaeontology, No. GG 21002.

*Dimensions of lectotype.* — Height 35.2 mm; maximum diameter 14.1 mm.

*Type locality.* — Ranikot, Sind, Pakistan. Late Paleocene.

The lectotype (Pl. 16, figs. 12-14) is an immature specimen; the paralectotype is larger but badly preserved, and does not show the axial sculpture well. The specimen figured by d'Archiac and Haime (1854, pl. 32, figs. 22) (see Pl. 16, figs. 15-17) does not represent *M. plicata.* It was questionably reidentified as *Terebellum carcassense* Leymerie ? by Cox (1931b, p. 51) and is here tentatively placed in the synonymy of *Seraphs sopitus* (Solander).

So far *M. plicata* has been found only in the upper Ranikot beds of Sind, which are of late Paleocene age according to Nagappa (1959, p. 150) and Adams (1970, fig. 2). A well-preserved specimen from the upper Ranikot beds of an unspecified locality of Sind, Pakistan, is here figured (Pl. 16, figs. 1-4). Attached to the matrix in its aperture is a specimen of *Assilina ranikoti* Nuttall (identification by H. Schaub). This specimen has served for the above description of the species as it shows sculptural details and the canal extending across the apex. Only the lower part of its body whorl is not well preserved, and the base of the columella is missing. The canal across the apex is almost closed, *i.e.* the connection with the outside is maintained by means of a narrow slit.

So far *M. plicata* is the only species of the genus. The species mentioned below should be considered as a *nomen dubium.*

*Distribution.* — Late Paleocene of Sind, Pakistan.

### **Mauryna costata** Martin

*Terebellum (Mauryna) costatum* Martin, 1931, Wetenschappelijke Meded., No. 18, p. 38, pl. 5, figs. 12, 12a (Upper Eocene, Java).

*Holotype.* — Repository unknown.

*Dimensions of holotype.* — Height about 24 mm; maximum diameter about 8 mm.

*Type locality.* — Kali Puru, Java. Upper Eocene.

Martin based his species on a single, incomplete, and somewhat crushed specimen which does not allow for the recognition of many morphological details. The figures he published of it are unsatisfactory. This specimen, the holotype of the species, is not deposited at the Rijksmuseum van Geologie en Mineralogie in Leiden, Holland, where most of Martin's material is kept. I was informed that it might be available in Bandung, Java.

Under such circumstances it is suggested that *M. costata* be treated as a *nomen dubium* until better topotype material becomes available.

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# PLATES

## EXPLANATION OF PLATE 1

*Figure* **Page**

1-19. *Seraphs (Seraphs) sopitus* (Solander) .......... 16

1-3. Lectotype of *Bulla sopita*. Brit. Mus. (Nat. Hist.), Dept. of Palaeont., No. GG 21010. Height 26.4 mm. Specimen figured by Solander (1766, pl. 1, fig. 29a) from Hordwell near Barton, upper Eocene. Photographs courtesy British Museum (Natural History) ; 4 ×.

4-5. NMB No. H 14492. Height 38.9 mm, diameter 12.6 mm. Grignon, west of Paris, Lutetian; 2 ×.

6. NMB No. H 14494. Height 23.3 mm, diameter 8.4 mm. Villiers-St-Frédéric near Paris, Lutetian; 2 ×.

7-9. NMB No. H 15406. Height 25.7 mm, diameter 9.4 mm. Barton, upper Eocene. Same specimen as that shown in Text-figure 11; 2 ×.

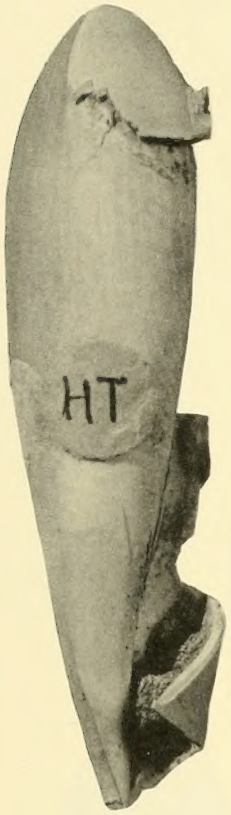
10-11. NMB No. H 14483. Height 19.8 mm, diameter 7.5 mm. Villiers-St-Frédéric near Paris, Lutetian. Note dots of original colour pattern; 2 ×.

12-13. NMB No. H 14493. Height 21.2 mm, diameter 7.3 mm. Grignon, west of Paris, Lutetian. Note remnants of colour pattern; 2 ×.

14-15. NMB No. H 16525. Height 29.1 mm, diameter 10.5 mm. Barton, southern England, upper Eocene; 2 ×.

16-17. NMB No. H 15404. Height 14.4 mm, diameter 5.8 mm. Grignon, west of Paris, Lutetian. Note accentuated growth lines; 4 ×.

18-19. NMB No. H 14495. Height 65.2 mm, diameter 23.6 mm. Barton, southern England, upper Eocene; 1.5 ×.



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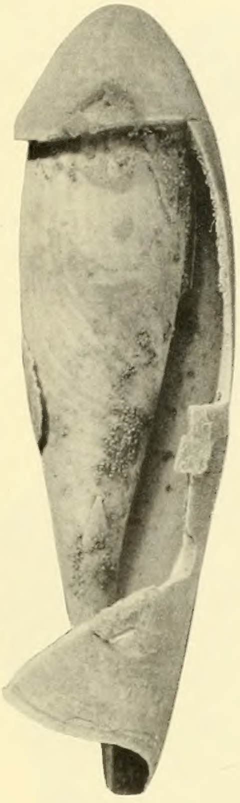

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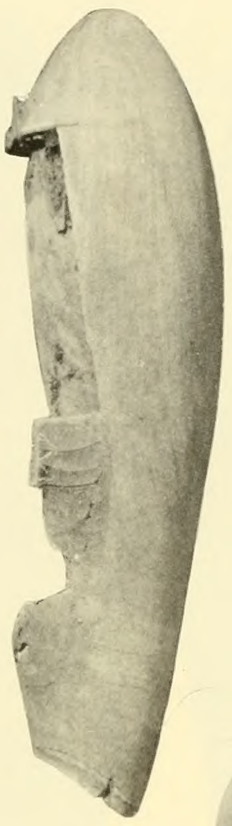

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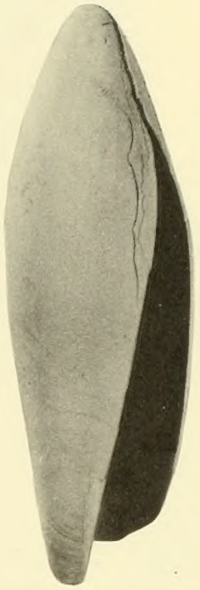

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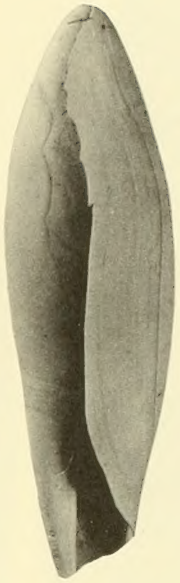

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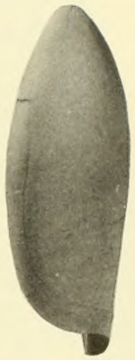

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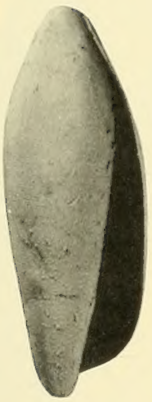

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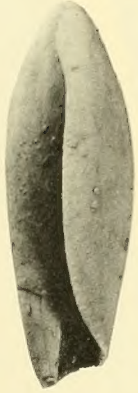

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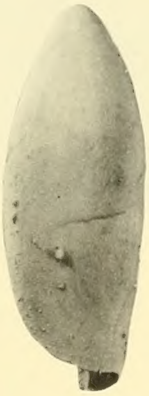

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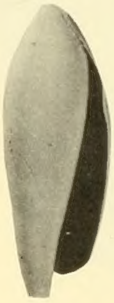

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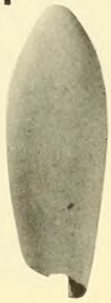

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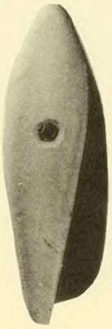

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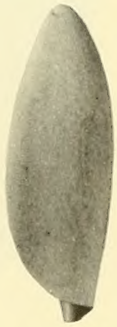

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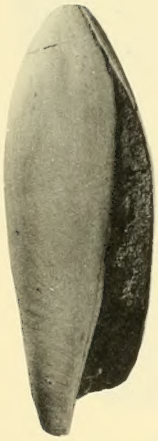

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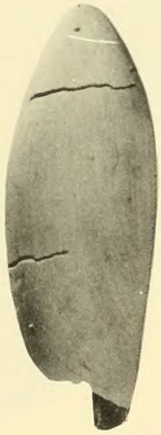

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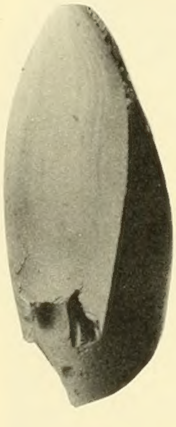

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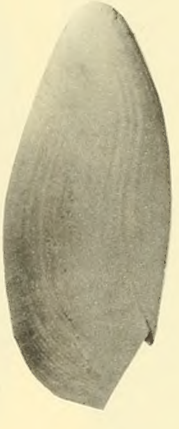

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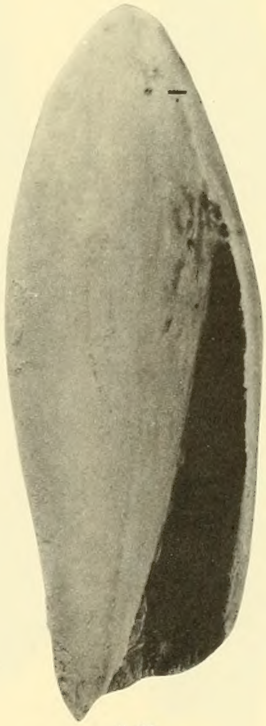

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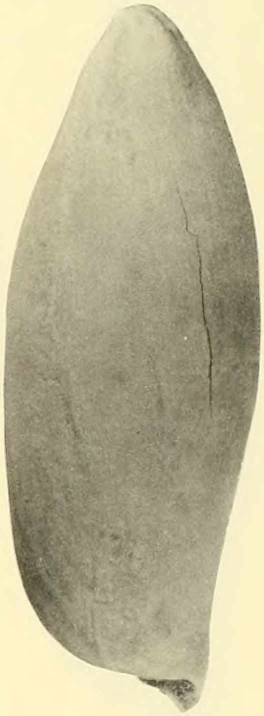

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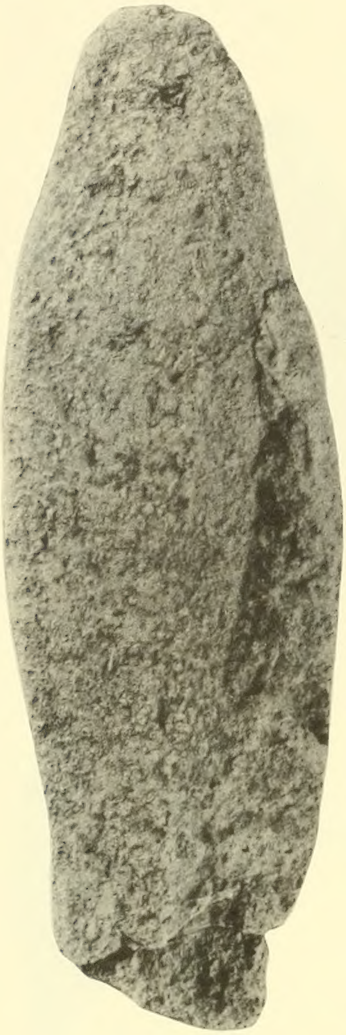
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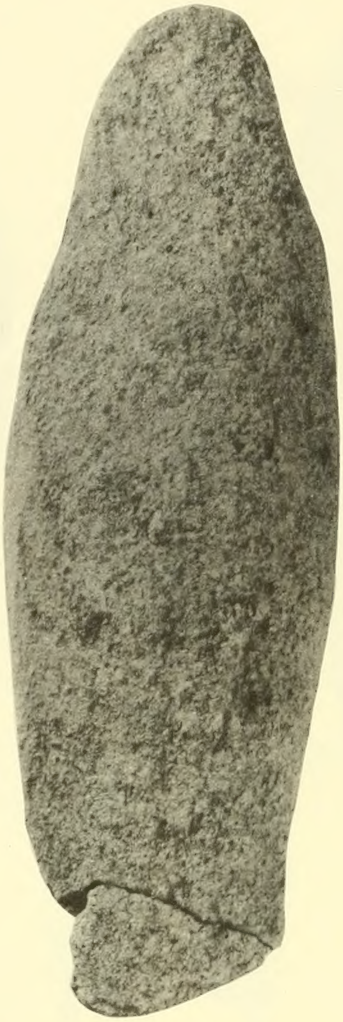
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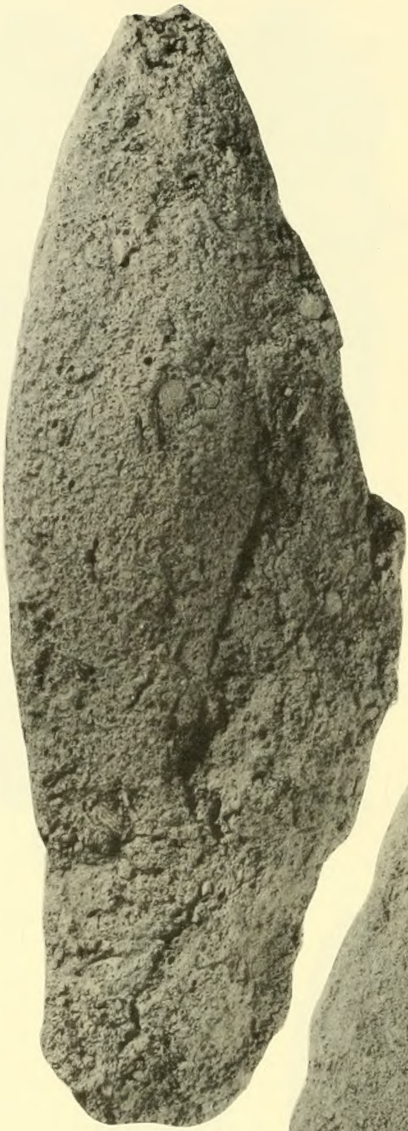
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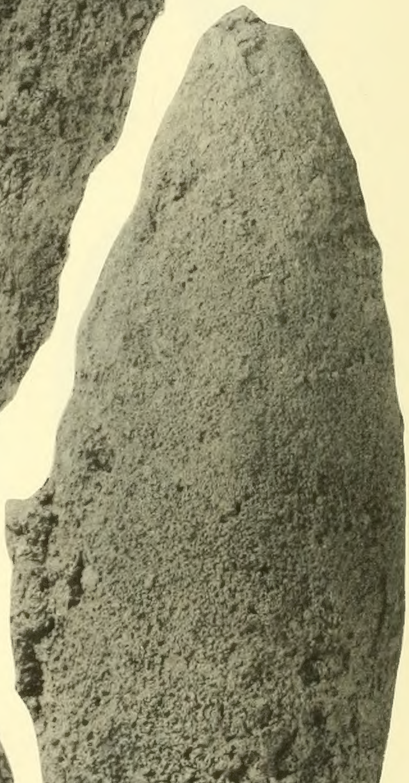
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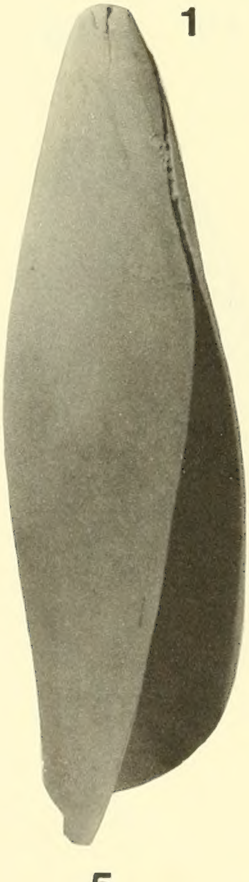
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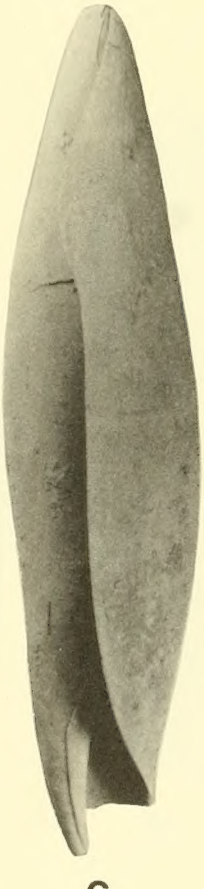
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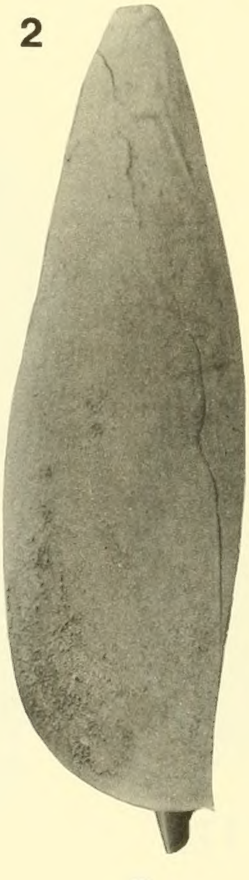
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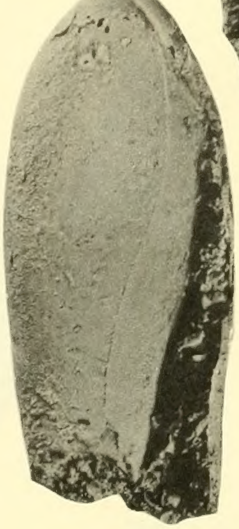
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## EXPLANATION OF PLATE 2

*Figure* *Page*

1-8. *Seraphs (Seraphs) sopitus* (Solander) .......... 16

1-2. NMB No. H 16542. Height 93.0 mm, diameter 31.0 mm. Monoster, Cluj basin, Rumania, upper (?) Eocene; 1.5 ×.

3-4. NMB No. H 16541. Height 102.7 mm, diameter 36.4 mm. Mokattam near Cairo, Egypt, middle Eocene. Specimens of *Nummulites beaumonti* and *N. lyelli* on the steinkern point to a Biarritzian (late middle Eocene) age (information from H. Schaub); 1.5 ×.

5-7. NMB No. H 14501. Height 77.9 mm, diameter 22.5 mm. Chaussy, NW of Paris, Lutetian; 1.5 ×.

8. NMB No. H 16596. Height 37.0 mm, diameter 15.6 mm. Monte Postale, northern Italy, early Eocene; 2 ×.

## EXPLANATION OF PLATE 3

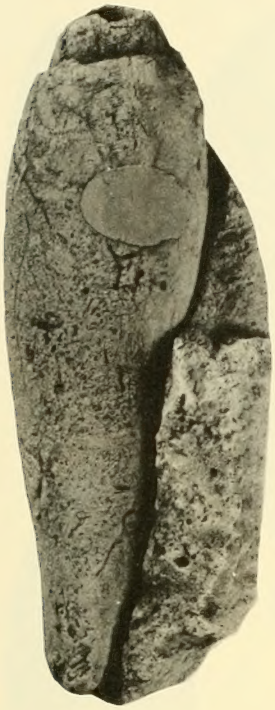
| Figure | | Page |
|---|---|---|
| 1-9. | *Seraphs (Seraphs) sopitus* (Solander) | 16 |

1-3. Holotype of *Terebellum subbelemnitoideum* d'Archiac and Haime (1854, p. 333, pl. 32, figs. 16, 16a). Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. GG 21001. Height 62.2 mm, diameter 24.2 mm. Laki beds of Sind, early Eocene; 1.5 ×.

4-5. Type specimen of *Terebellum fusiforme* Lamarck, which is an internal cast of *S. sopitus* (see comments under *Paraseraphs tetanus*). Copy of figures published by Favre (1918, pl. 13, figs. 209a, b). Locality and horizon not known. Specimen in collections of Natural History Museum, Geneva; 1.5 ×.

6-8. Lectotype of *Terebellum belemnitoideum* d'Archiac (*in* Tchihatcheff, 1850, p. 405). Muséum National d'Histoire Naturelle, Paris, No. B 22388. Height 83.2 mm, diameter 30.1 mm. Zafranboli, Turkey, probably Lutetian; 1.5 ×.

9. NMB No. H 14517. Height 80.8 mm, diameter 27.6 mm. Roncá, northern Italy, late middle Eocene. Topotype of *Terebellum convolutum roncanum* de Gregorio; 1.5 ×.



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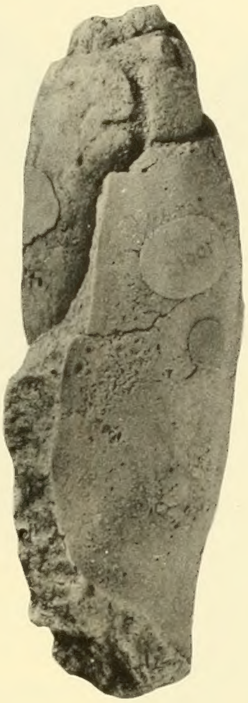

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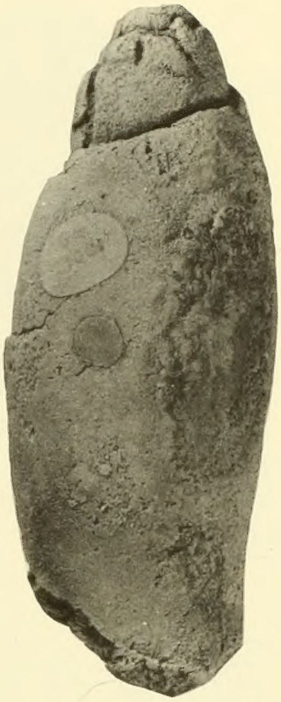

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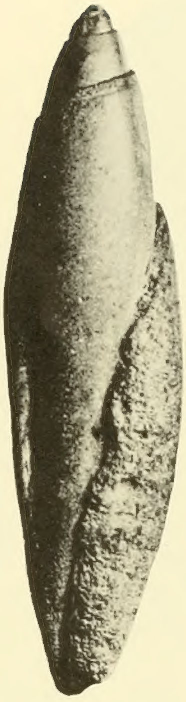

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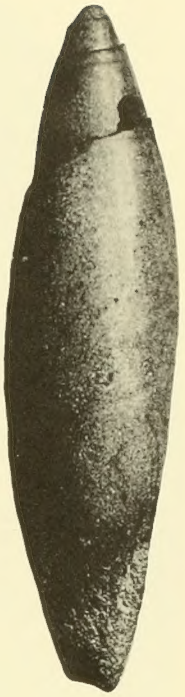

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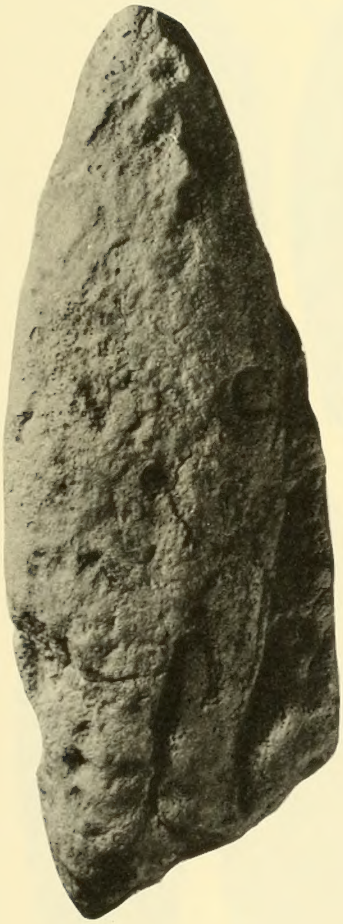

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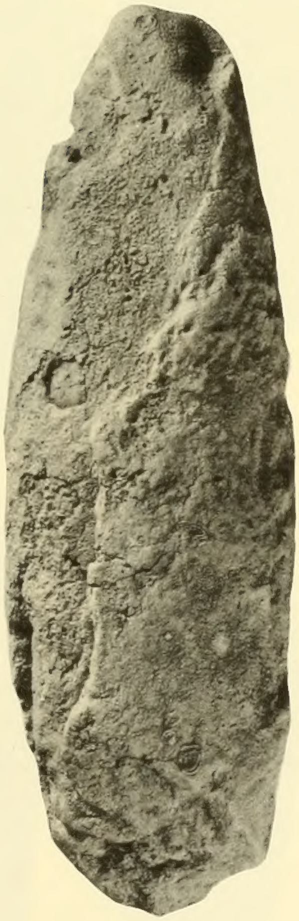

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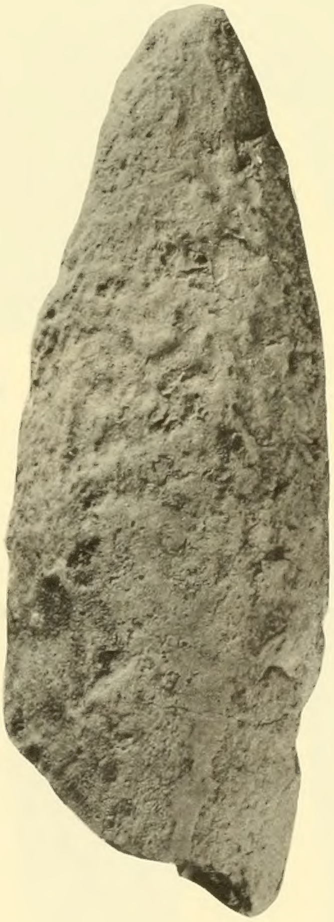

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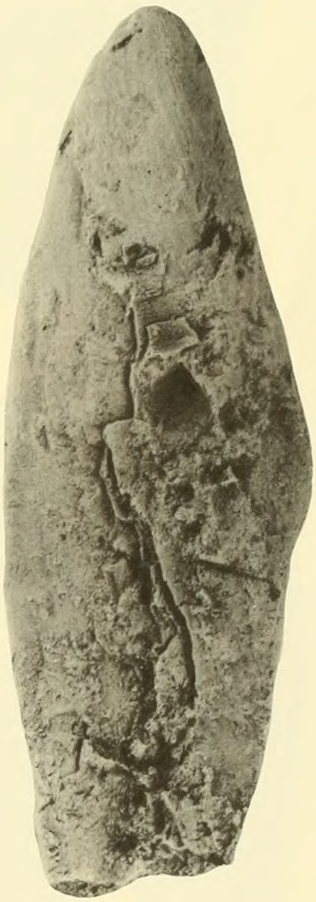

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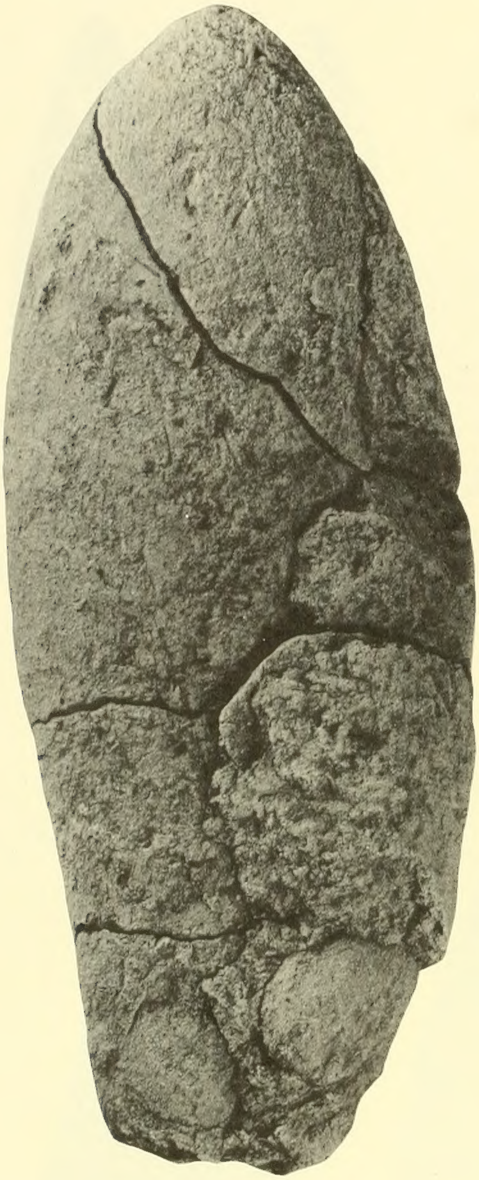

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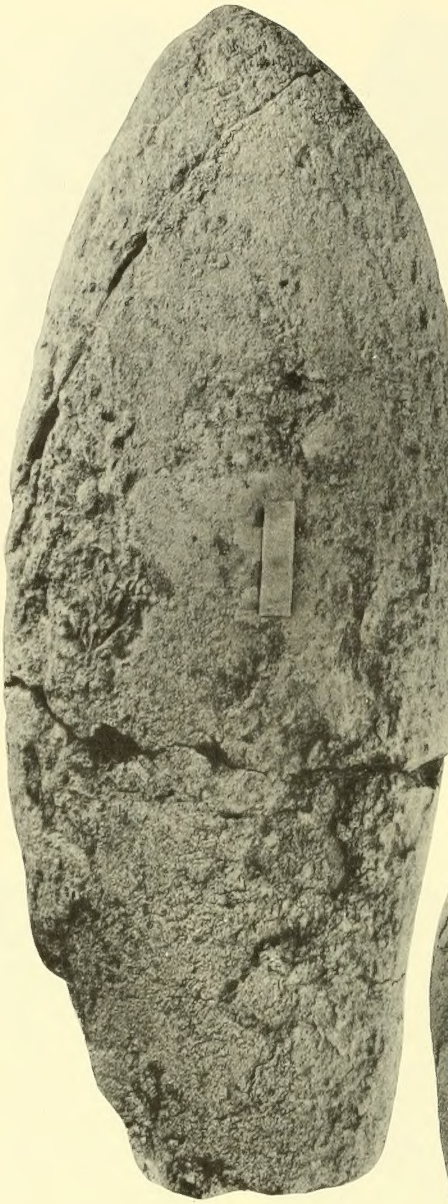

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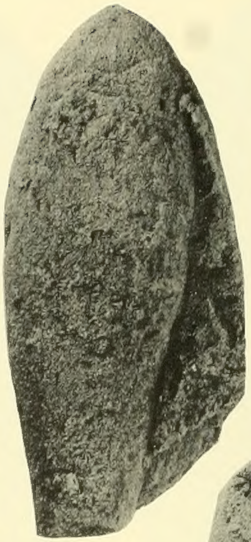

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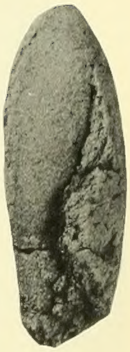

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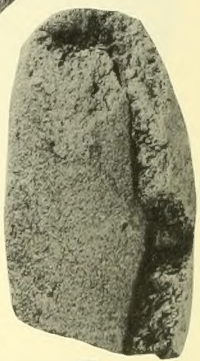

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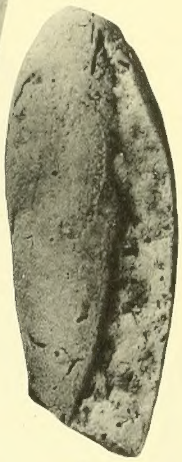

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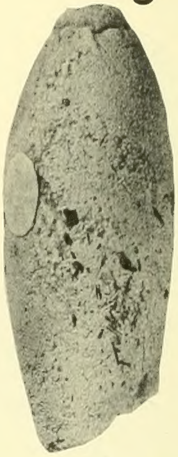

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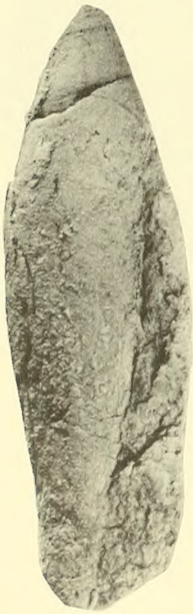

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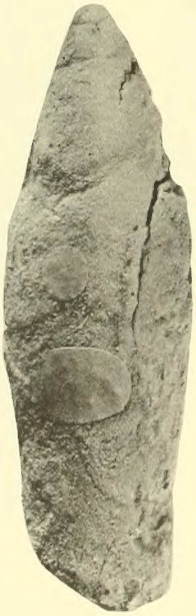

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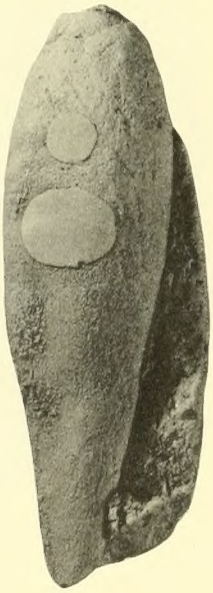

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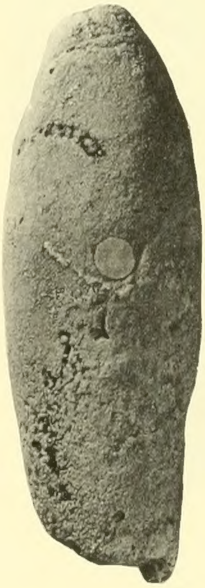

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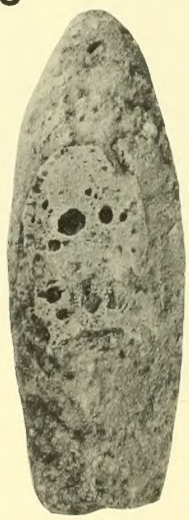

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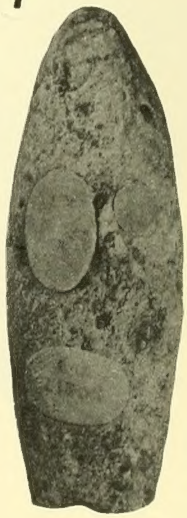

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## EXPLANATION OF PLATE 4

*Figure* *Page*

1-13. *Seraphs (Seraphs) sopitus* (Solander) ........ 16

1-2. Lectotype of *Terebellum obesum* Mayer (1866, pp. 320, 333). NMB No. H 16594. Height 108.4 mm, diameter 42.0 mm. Djulfa, Armenia, probably middle Eocene; 1.5 ×.

3. Paralectotype of *Terebellum obesum* Mayer (1866, pp. 320, 333). NHB No. H 16595. Height 48.2 mm, diameter 22.3 mm. Djulfa, Armenia, probably middle Eocene; 1.5 ×.

4. Paralectotype of *Terebellum obesum* Mayer (1866, pp. 320, 333). NMB No. H 16598. Height 31.1 mm, diameter 11.0 mm. Djulfa, Armenia, probably middle Eocene; 1.5 ×.

5. Syntype of *Terebellum oliviforme* Mayer (1866, p. 332). NMB No. H 16597. Height 31.6 mm, diameter 17.1 mm. This is questionably taken into the synonymy of *S. sopitus*. Akhaltsikhe near Tiflis, Georgia, USSR, Bartonian; 1.5 ×.

6-7. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No G 50181. Height 39.7 mm, diameter 15.3 mm. This specimen had been studied by Cox (1931b) and identified as *T. carcassense*. Laki beds of Sind, early Eocene; 1.5 ×.

8-9. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. G 68233. Height 52.2 mm, diameter 16.7 mm. Figured by Eames (1952, p. 74, pl. 3, figs. 76a, b) as *T. fusiformopse* Gregorio. Middle Eocene White marl Band with *Discocyclina sowerbyi*, Zinda Pir, Pakistan; 1.5 ×.

10-11. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. G 50180. Height 51.3 mm, diameter 17.7 mm. Figured by Cox (1931b, pl. 1, fig. 21) as *Terebellum carcassense* Leymerie. Laki beds of Sind, early Eocene; 1.5 ×.

12-13. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. GG 21009. Height 44.7 mm, diameter 15.7 mm. Figured by d'Archiac and Haime (1854, pl. 32, fig. 20) as *Terebellum obtusum* J. de C. Sowerby. This specimen was reidentified by Cox (1931b, p. 52) as *Terebellum carcassense* Leymerie. Laki beds of Sind, early Eocene; 1.5 ×.

## EXPLANATION OF PLATE 5

*Figure* *Page*

1-2. *Seraphs (Seraphs)* sp. .......... 20
Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. G 50388. Height 38.5 mm, diameter 16.0 mm. Specimen described and figured by Cox (1931b, p. 52, pl. 1, fig. 16) as *Terebellum* sp. Laki beds of Sind, early Eocene; 1.5 ×.

3-4. *Seraphs (Seraphs)* cf. *sopitus* (Solander) .......... 21
NMB No. H 16546. Artificial cast of U.S. Nat. Mus., No. 135098. Height 50.6 mm, diameter 18.5 mm. Near Port Antonio, Portland, Jamaica, middle or late Eocene; 1.5 ×.

5-9. *Seraphs (Seraphs) olivaceus* (Cossmann) .......... 21
5-7. NMB No. H 16518. Height 28.7 mm, diameter 8.4 mm. Chaussy, NW of Paris, Lutetian; 2 ×.

8-9. NMB No. H 16520. Height 24.4 mm, diameter 7.6 mm. Chaussy, NW of Paris, Lutetian; 2 ×.

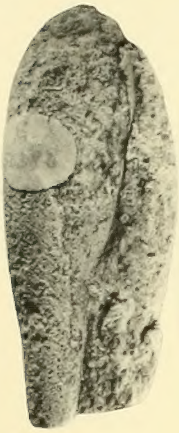
10-11. *Seraphs (Seraphs) olivaceus* (Cossmann) ? .......... 21
NMB No. H 15407. Height 32.2 mm, diameter 9.7 mm. Piana, west of Schio, northern Italy, Lutetian; 2 ×.

12-21. *Seraphs (Seraphs) chilophorus* (Cossmann) .......... 22
12-14. NMB No. H 16512. Height 21.2 mm, diameter 6.3 mm. Chaussy, NW of Paris, Lutetian; 3 ×.

15-16. NMB No. H 16504. Height 19.9 mm, diameter 6.3 mm. Chaussy, NW of Paris, Lutetian; 3 ×.

17-19. NMB No. H 16505. Height 24.2 mm, diameter 7.4 mm. Chaussy, NW of Paris, Lutetian; 3 ×.

20-21. NMB No. H 16515. Height 26.6 mm, diameter 8.0 mm. Chaussy, NW of Paris, Lutetian; 3 ×.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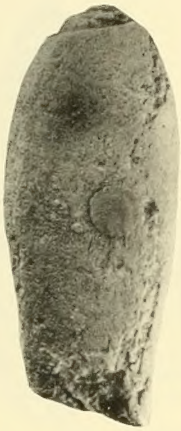
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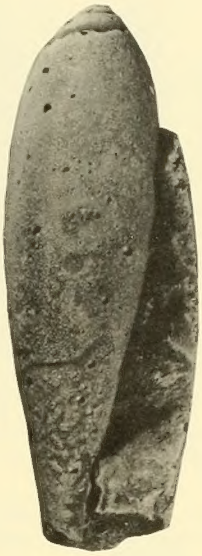
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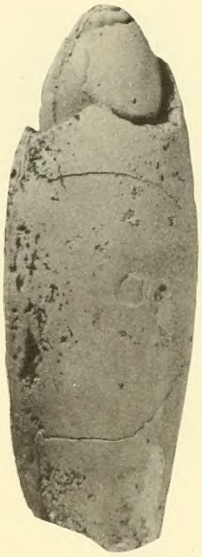
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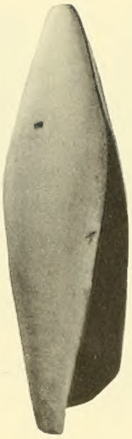
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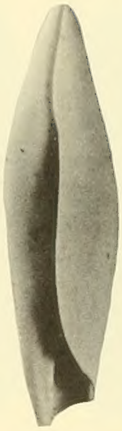
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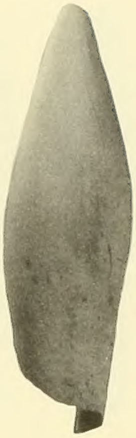
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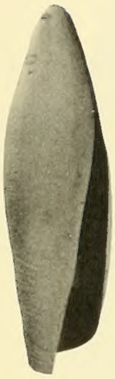
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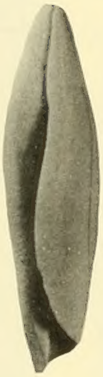
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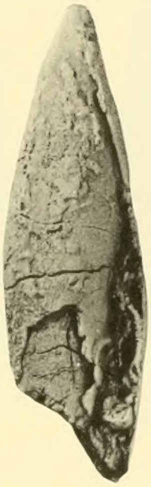
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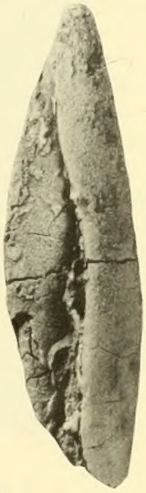
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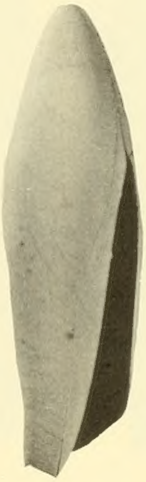
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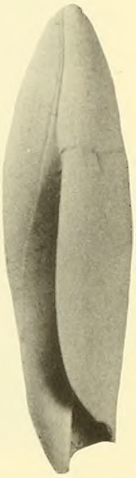
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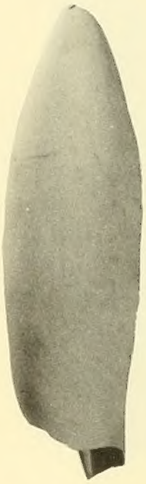
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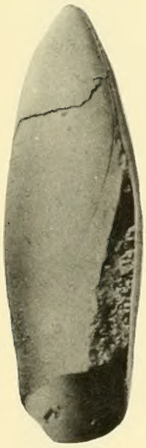
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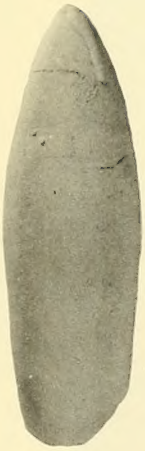
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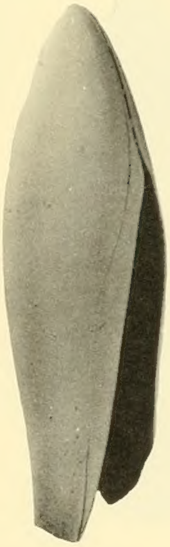
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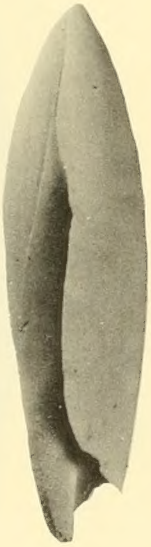
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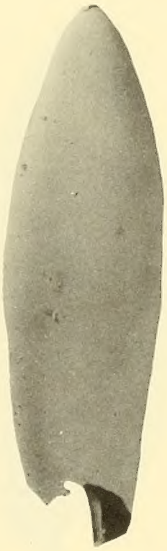
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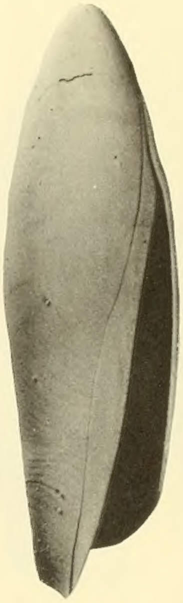
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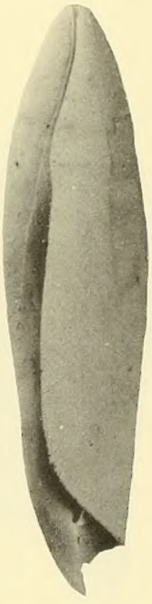
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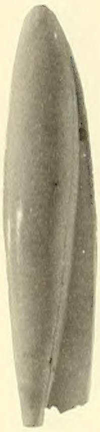
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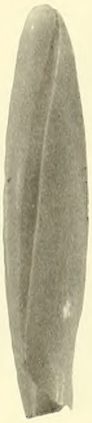
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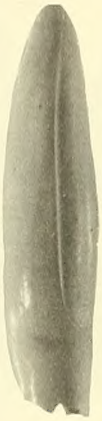
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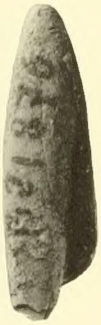
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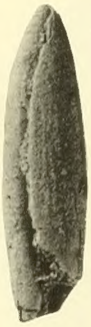
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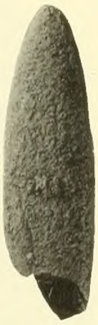
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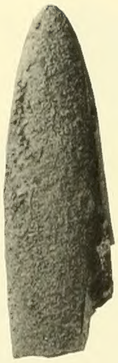
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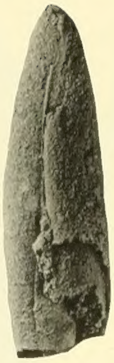
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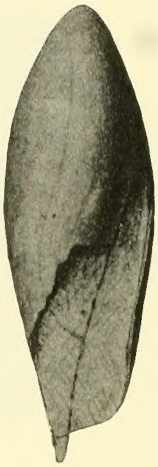
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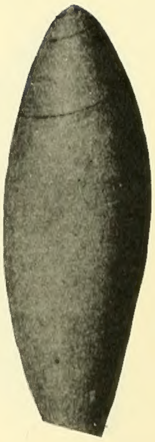
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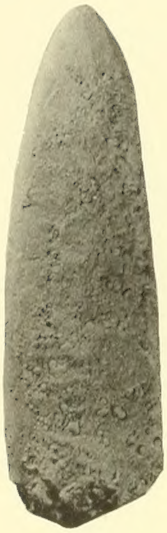
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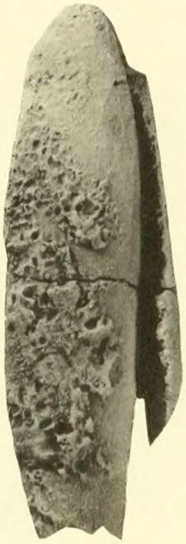
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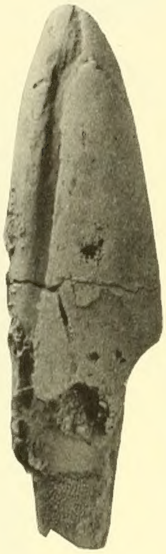
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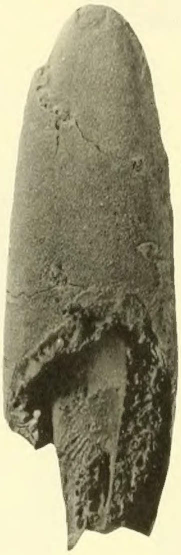
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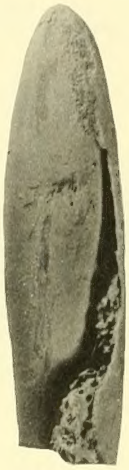
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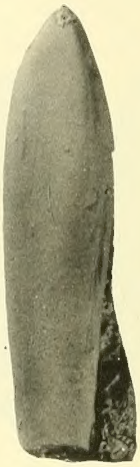
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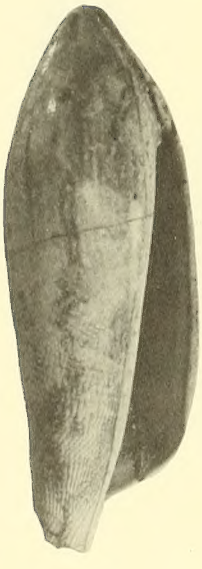
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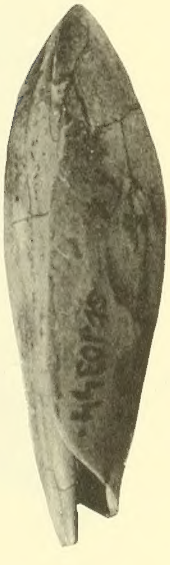
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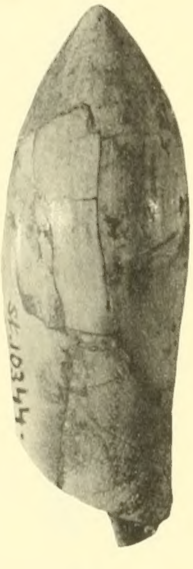
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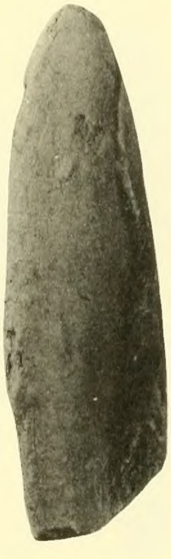
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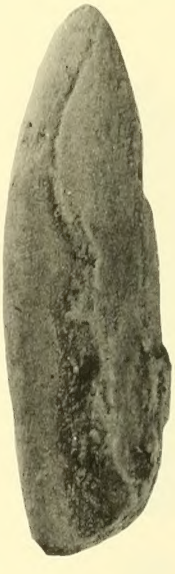
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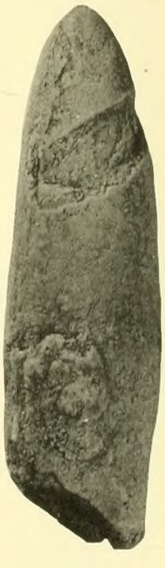
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## EXPLANATION OF PLATE 6

*Figure* *Page*

1-3. *Seraphs (Seraphs) leukoleptus*, n. sp. .......... 23
Holotype. Ecole des Mines de Paris, Laboratoire de paléontologie, unnumbered. Coll. Deshayes. Height 27.6 mm, diameter 6.2 mm. Chaussy, NW of Paris, Lutetian; 2 ×.

4-8. *Seraphs (Seraphs) leukoleptus*, n. sp. ? .......... 24
4-6. Muséum National d'Histoire Naturelle, Paris, No. B 21876. Height 21.2 mm, diameter 6.4 mm. San Giovanni Ilarione, northern Italy, Lutetian; 2 ×.

7-8. Muséum National d'Histoire Naturelle, Paris, No. B 21876. Height 23.7 mm, diameter 7.3 mm. San Giovanni Ilarione, northern Italy, Lutetian; 2 ×.

9-10. *Seraphs (Seraphs) minus* (Vincent) .......... 25
Musée de l'Afrique Central, Tervuren, Belgium ? Copy of original figures. Landana, Cabinda, Angola, Paleocene; 7.5 ×.

11-16. *Seraphs (Seraphs) belemnitus* (Palmer) .......... 25
11. NMB No. H 16574. Artificial cast of holotype. Height 49 mm, diameter 15 mm. Florida Geol. Survey locality L-93: Gulf Hammock, northern Florida, late Eocene; 1.5 ×.

12-14. Paleont. Research Inst., Ithaca, N.Y., No. 29236. Height 48.2 mm, diameter 15.8 mm. Topotype, late Eocene of northern Florida; 1.5 ×.

15-16. Paleont. Research Inst., Ithaca, N.Y., No. 29236. Height 41.1 mm, diameter 11.4 mm. Topotype, late Eocene of northern Florida; 1.5 ×.

17-19. *Seraphs (Seraphs) squamosus* (Martin) .......... 25
Lectotype. Rijksmuseum van Geologie en Mineralogie, Leiden, No. St. 10344. Height 37.1 mm, diameter 13.1 mm. Kali Puru, Nanggulan, Res. Djokjakarta, Java: "upper Eocene". Photograph courtesy Rijksmuseum van Geologie en Mineralogie, Leiden; 2 ×.

20-22. *Seraphs (Seraphs) naricus* (Vredenburg) .......... 28
NMB No. H 15420. Artificial cast of holotype, Central Palaeont. Labs., Geol. Survey India, Calcutta, No. 12614. Height 38.6 mm, diameter 10.8 mm. Bhagothoro Hill, Sind, Pakistan, Nari beds (Oligocene); 2 ×.

## EXPLANATION OF PLATE 7

*Figure* *Page*

1-17. *Seraphs (Seraphs) plicifer* (Bayan) .......... 24

1-4. Paralectotype. Ecole des Mines de Paris, Laboratoire de paléontologie, No. G 2102. Height 43.8 mm, diameter 16.0 mm. Specimen figured by Bayan (1870b, pl. 8, fig. 2), Pozza near San Giovanni Ilarione, northern Italy, Lutetian; 2 ×.

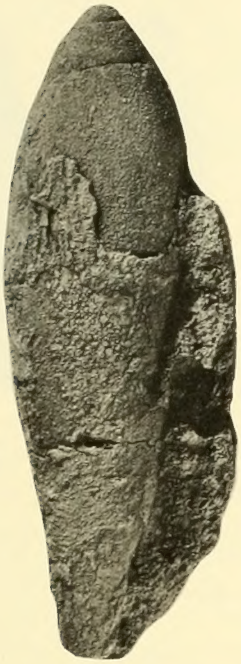
5-7. Lectotype. Ecole des Mines de Paris, Laboratoire de paléontologie, No. G 2100. Height 33.7 mm, diameter 13.9 mm. Specimen figured by Bayan (1870b, pl. 8, fig. 1). Croce Grande near San Giovanni Ilarione, northern Italy, Lutetian; 2 ×.

8. Paralectotype. Ecole des Mines de Paris, Laboratoire de paléontologie, No. G 2101. Height 14.6 mm, diameter 5.4 mm. Croce Grande near San Giovanni Ilarione, northern Italy, Lutetian; 2 ×.

9-12. Muséum National d'Histoire Naturelle, Paris, No. B 21878. Height 43.5 mm, diameter 16.4 mm. San Giovanni Ilarione, northern Italy, Lutetian; 2 ×.

13-15. NMB No. H 14504. Height 32.8 mm, diameter 10.9 mm. Piana-Cornedo, west of Schio, northern Italy, Lutetian; 2 ×.

16-17. NMB No. H 14506. Height 34.0 mm, diameter 12.1 mm. Piana-Cornedo, west of Schio, northern Italy, Lutetian; 2 ×.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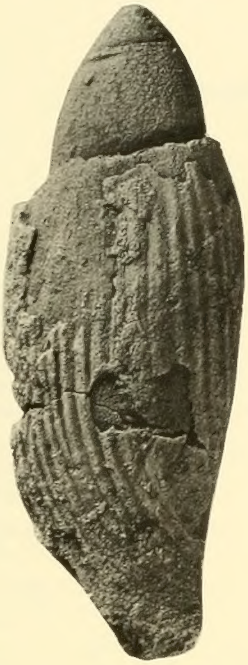
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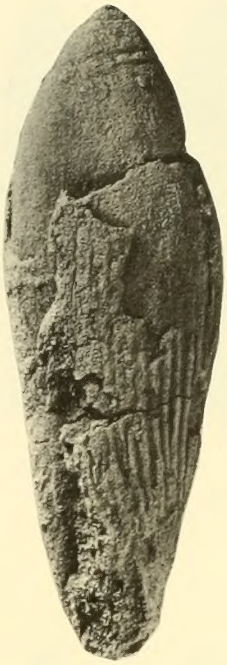
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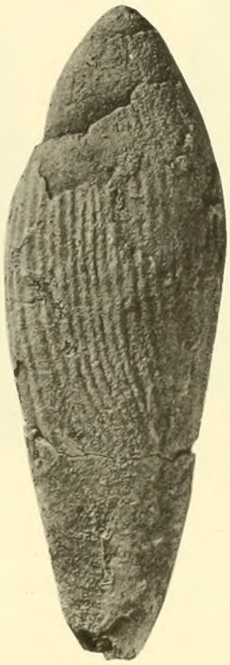
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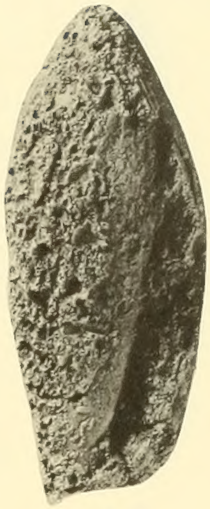
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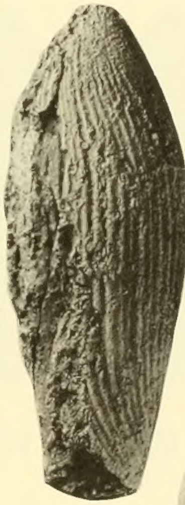
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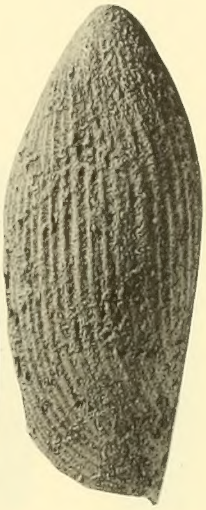
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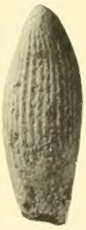
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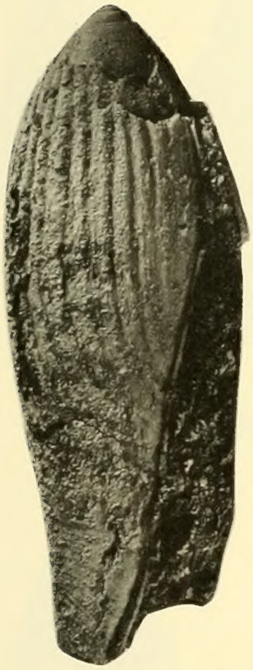
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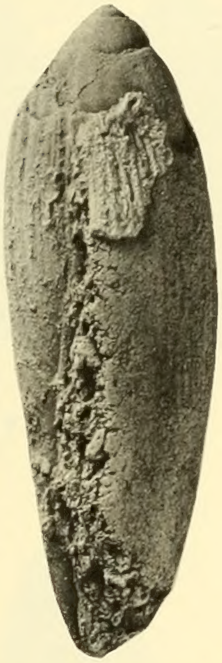
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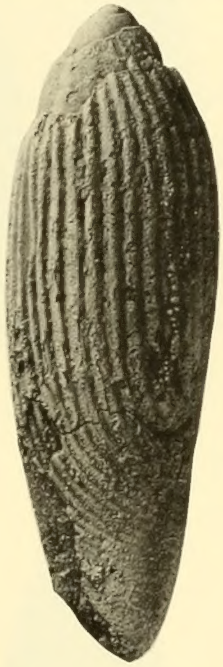
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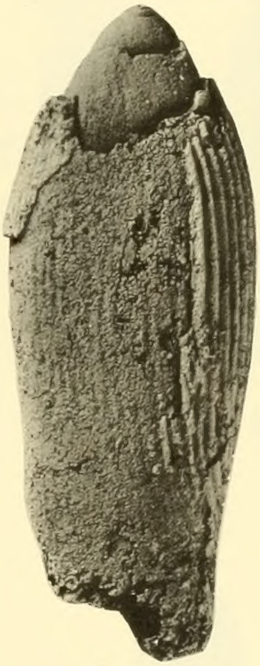
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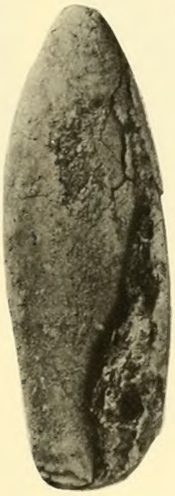
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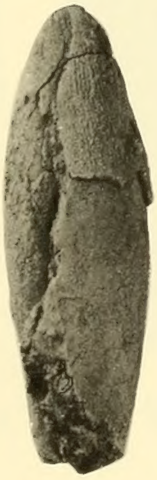
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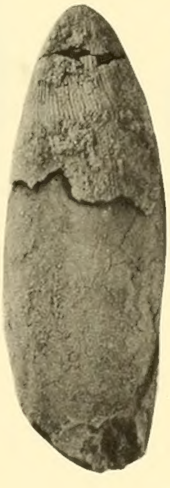
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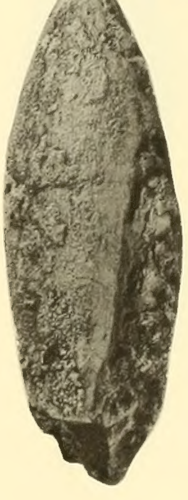
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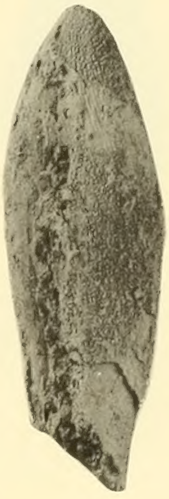
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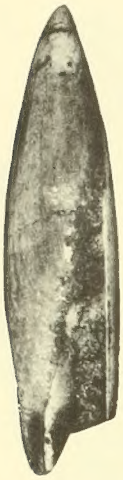
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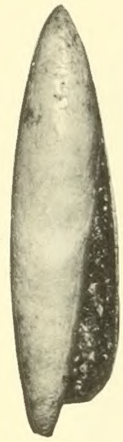
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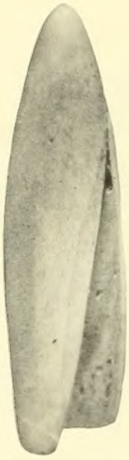
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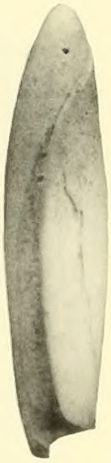
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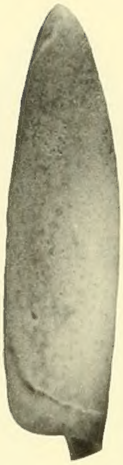
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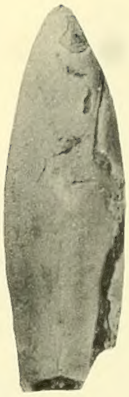
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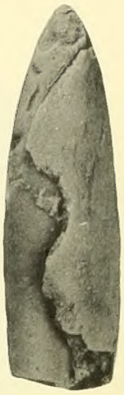
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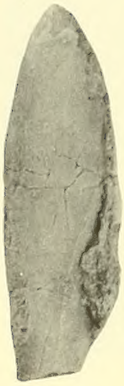
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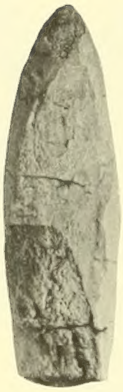
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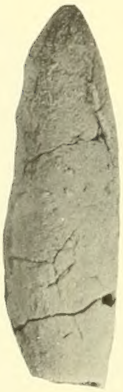
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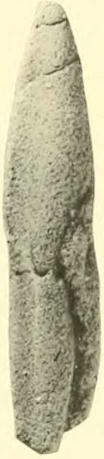
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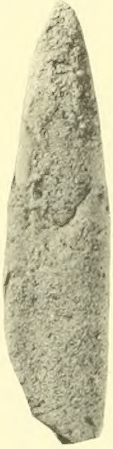
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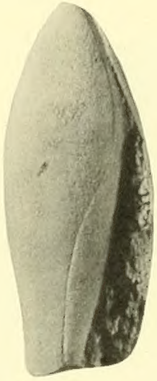
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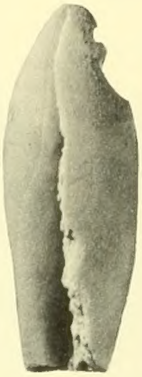
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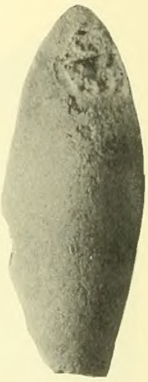
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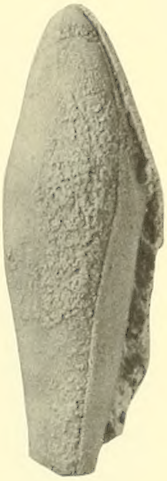
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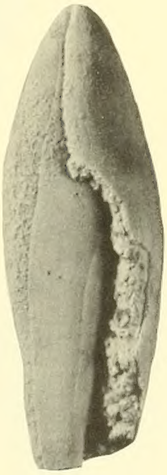
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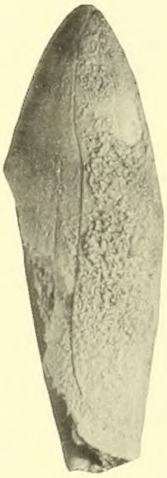
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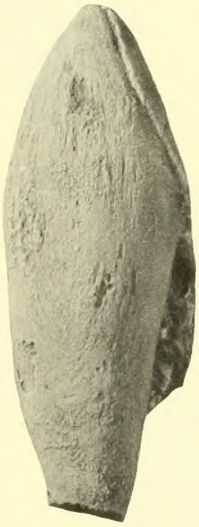
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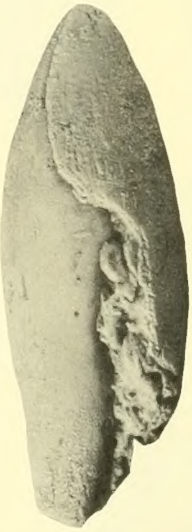
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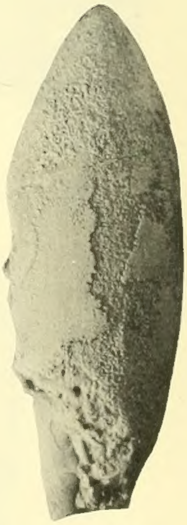
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## EXPLANATION OF PLATE 8

*Figure* *Page*

1-10. *Seraphs (Seraphs) subconvolutus* (d'Orbigny) ........ 26

1. Holotype of *Terebellum subfusiformis* d'Orbigny. Grateloup collection, Laboratoire de Géologie, Bordeaux, unnumbered. Height 30 mm, diameter 7 mm. Dax, Lesbarritz, Aquitaine basin, France, Stampian (Oligocene); 2 ×.

2. Neuville collection, Institut de Géologie du Bassin d'Aquitaine, Talence, Gironde, France, unnumbered. Height 28 mm, diameter 7 mm. Gaas, Lesbarritz, Aquitaine basin, France, Stampian (Oligocene); 2 ×.

3-5. Neuville collection, Institut de Géologie du Bassin d'Aquitaine, Talence, Gironde, France, unnumbered. Height 29 mm, diameter 7.5 mm. Gaas, Lesbarritz, Aquitaine basin, France, Stampian (Oligocene); 2 ×.

6-7. NMB No. H 16576. Height 25.7 mm, diameter 8.1 mm. Castelgomberto, northern Italy, Oligocene; 2 ×.

8-10. NMB No. H 16577. Height 25.1 mm, diameter 8.1 mm. Castelgomberto, northern Italy, Oligocene; 2 ×.

11-12. *Seraphs (Seraphs)* cf. *subconvolutus* (d'Orbigny) ........ 27

11. NMB No. H 14518. Height 29.7 mm, diameter 7.1 mm. Cassinelle, northern Italy, Tongrian (Oligocene); 2 ×.

12. NMB No. H 14519. Height 29.1 mm, diameter 7.0 mm. Cassinelle, northern Italy, Tongrian (Oligocene); 2 ×.

13-21. *Seraphs (Seraphs) mayeri*, n. sp. ........ 27

13-15. Paratype. NMB No. H 16579. Height 17.0 mm, diameter 7.0 mm. Monte Grumi near Castelgomberto, northern Italy, Oligocene; 3 ×.

16-18. Holotype. NMB No. H 16578. Height 21.4 mm, diameter 7.3 mm. Monte Grumi near Castelgomberto, northern Italy, Oligocene; 3 ×.

19-21. Paratype. NMB No. H 16580. Height 24.4 mm, diameter 9.2 mm. Monte Grumi near Castelgomberto, northern Italy, Oligocene; 3 ×.

## EXPLANATION OF PLATE 9

*Figure* *Page*

1-4. *Seraphs (Seraphs) striatus* (von Koenen) ........ 28
Copy of original figures. Height 38.5 mm, diameter 10.7 mm. Lattorf, Germany, lower Oligocene; 1.5 ×.

5-6. *Seraphs (Seraphs) andersoni* Dickerson ........ 29
5. Holotype. California Academy of Sciences, Dept. Geology, San Francisco, No. 434. Height 38.0 mm, diameter 11.0 mm. California Acad. Sci. locality 181: about 4 miles east of Vader, Lewis County, Washington, *Molopophorus lincolnensis* zone (lower Oligocene). Photograph courtesy California Academy of Sciences; 1 ×.

6. Paratype. California Academy of Sciences, Dept. Geology, San Francisco, No. 435. Height 41.9 mm, diameter 13.1 mm. California Acad. Sci. locality 181: about 4 miles east of Vader, Lewis County, Washington, *Molopophorus lincolnensis* zone (lower Oligocene). Photograph courtesy California Academy of Sciences; 1 ×.

7-9. *Seraphs* (?) *hernandoensis* (Mansfield) ........ 29
NMB No. H 16549. Artificial cast of holotype, U.S. Nat. Mus., No. 495948. Height 31.4 mm, diameter 9.5 mm. U.S Geol. Sur. locality 12318: near Brooksville, Hernando County, Florida, Suwannee limestone (Oligocene); 2 ×.

10-12. *Seraphs (Miniseraphs) eratoides* (Cossmann) ........ 30
NMB No. H 14503. Height 7.2 mm, diameter 4.2 mm. Chaussy, NW of Paris, Lutetian; 6 ×.

13-18. *Seraphs (Miniseraphs) isabella* (Deshayes) ........ 30
13-15. NMB No. H 14502. Height 15.4 mm, diameter 7.6 mm. Chaussy, NW of Paris, Lutetian; 3 ×.

16-18. NMB No. H 16545. Height 13.7 mm, diameter 6.7 mm. Chaussy, NW of Paris, Lutetian; 3 ×.

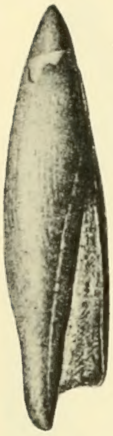
19-25. *Paraseraphs armoricensis* (Cossmann) ........ 36
19. Institut Royal des Sciences Naturelles de Belgique, Brussels, No. I.G. 10591. Height 38.0 mm, diameter 10.1 mm. Bois-Gouet, Loire-Inférieure, France, late middle Eocene; 1.5 ×.

20-21. NMB No. H 14507. Height 57.0 mm, diameter 10.4 mm. Monte Postale, northern Italy, early Eocene; 1.5 ×.

22-23. Holotype. Dumas collection, Museum of Nantes ? Height 73 mm, diameter 13 mm. Copy of figures published by Cossmann (1897, pl. 8, figs. 10, 15). Bois-Gouet, Loire-Inférieure, France, late middle Eocene; 1.5 ×.

24-25. Copy of figures edited by Cossmann in Vasseur (1880-1917, pl. 2, fig. 20, pl. 3, fig. 55). Bois-Gouet, Loire-Inférieure, France, late middle Eocene; 1.5 ×.

26. *Paraseraphs tetanus*, n. sp. ........ 34
NMB No. H 14547. Cuise-Lamotte, Dept. Oise, France: early Eocene. Axial section through protoconch showing evolute and involute stages; 30 ×.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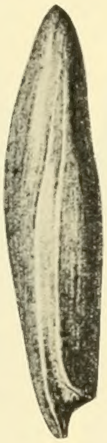
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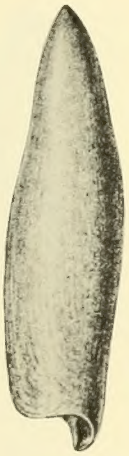
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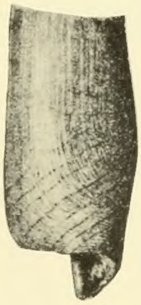
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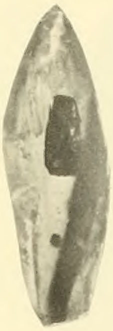
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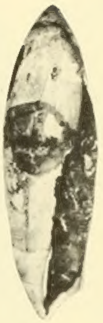
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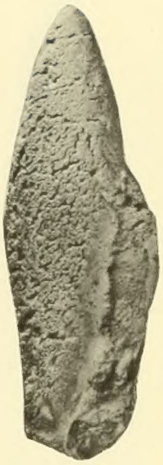
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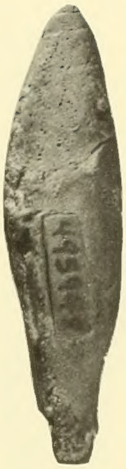
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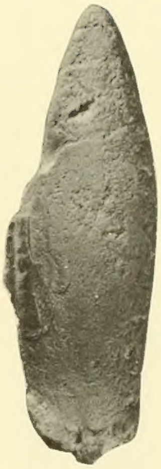
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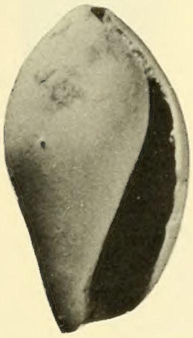
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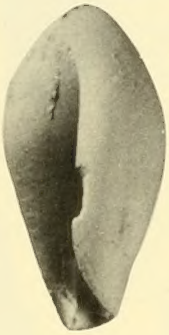
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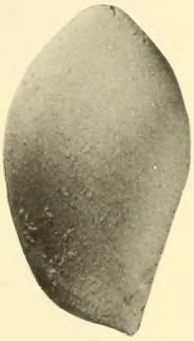
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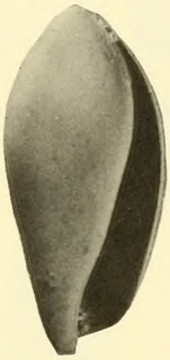
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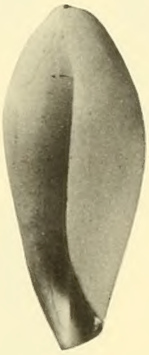
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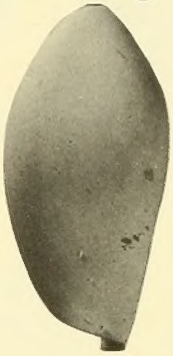
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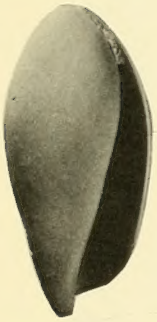
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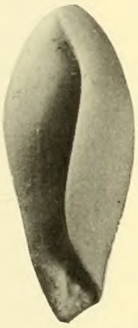
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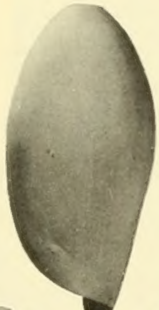
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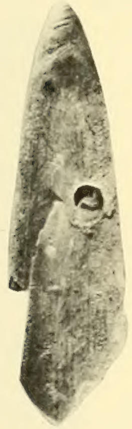
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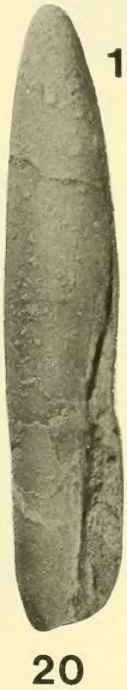
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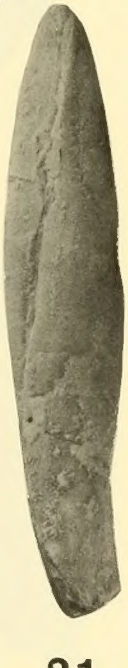
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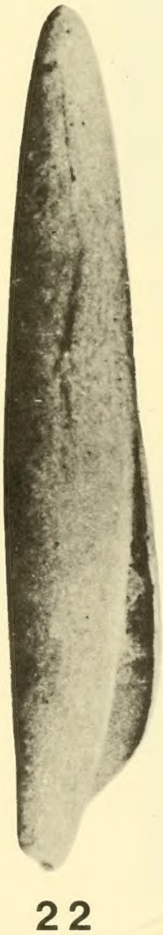
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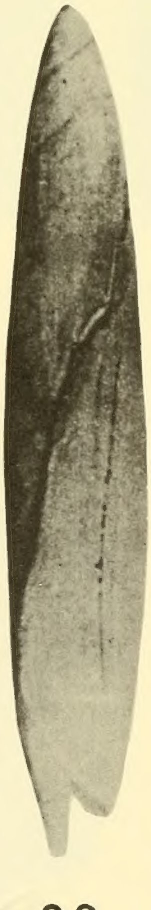
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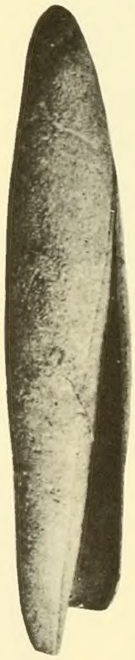
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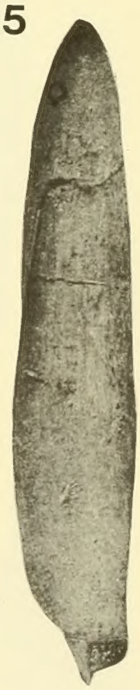
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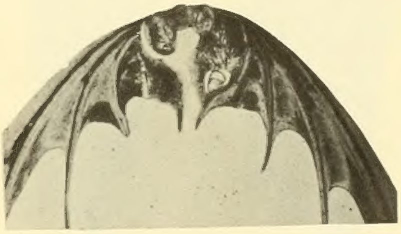
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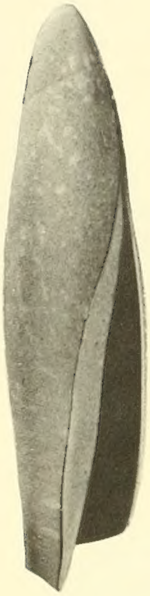
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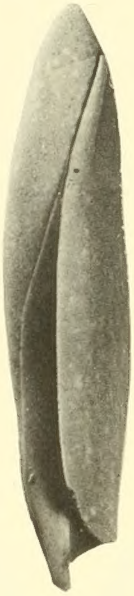
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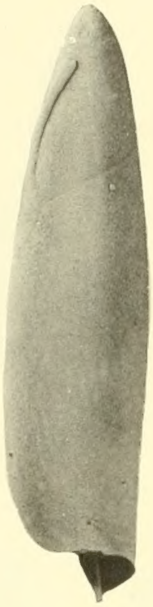
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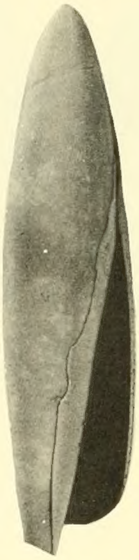
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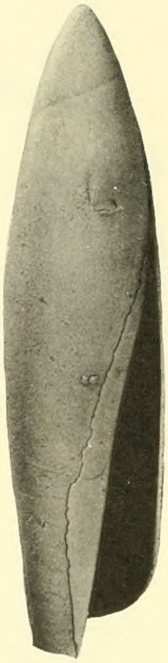
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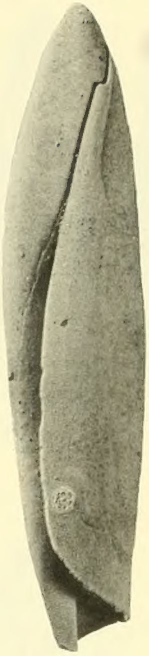
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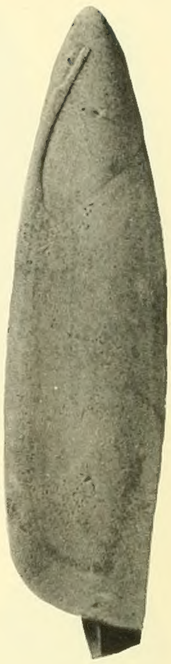
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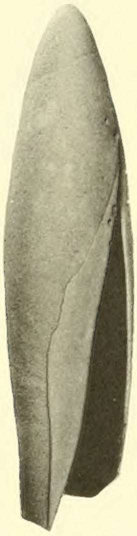
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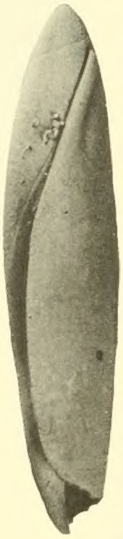
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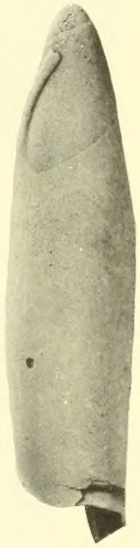
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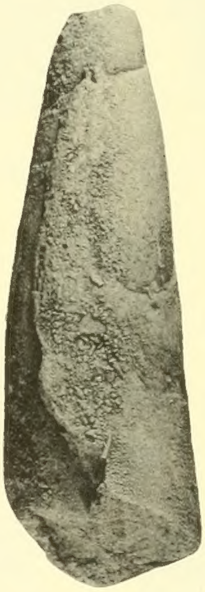
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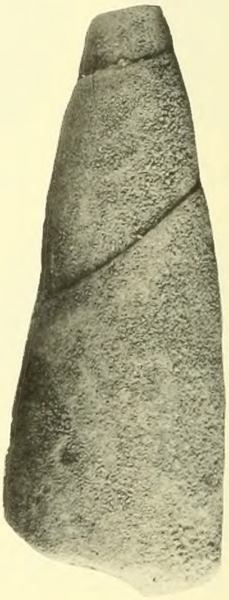
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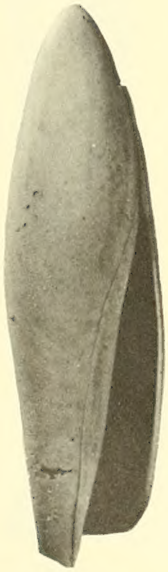
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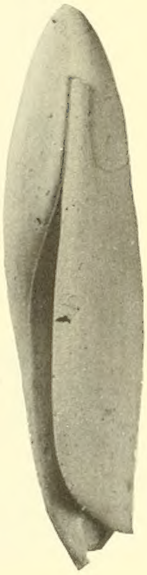
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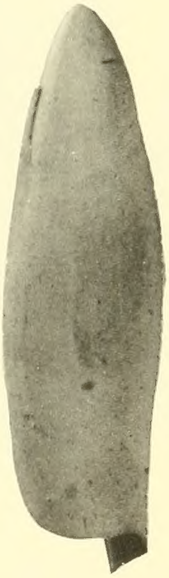
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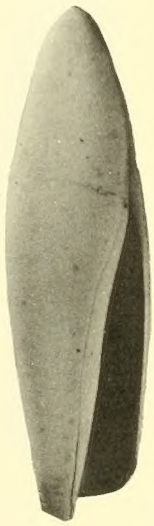
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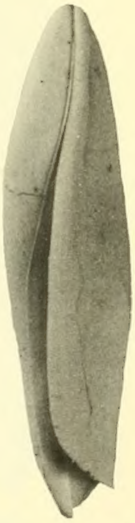
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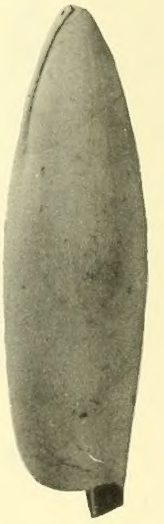
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## EXPLANATION OF PLATE 10

*Figure* *Page*

1-10. *Paraseraphs tetanus*, n. sp. ........ 34

1-3. Paratype. NMB No. H 15405. Height 26.4 mm, diameter 6.5 mm. Cuise-Lamotte, Dept. Oise, France, Cuisian (early Eocene). Same specimen as that shown in Text-figure 12; 3 ×.

4. Paratype. NMB No. H 15408. Height 24.3 mm, diameter 5.9 mm. Cuise-Lamotte, Dept. Oise, France, Cuisian (early Eocene); 3 ×.

5-7. Holotype. NMB No. H 15409. Height 28.7 mm, diameter 7.1 mm. Cuise-Lamotte, Dept. Oise, France, Cuisian (early Eocene); 3 ×.

8-10. Paratype. NMB No. H 16502. Height 23.5 mm, diameter 6.2 mm. Cuise-Lamotte, Dept. Oise, France, Cuisian (early Eocene); 3 ×.

11-12. *Paraseraphs* cf. *procerus* (Merian) ........ 39

NMB No. H 16584. Height 52.5 mm, diameter 21.3 mm. Manresa, Barcelona Province, Spain, late middle Eocene; 1.5 ×.

13-18. *Paraseraphs placitus*, n. sp. ........ 38

13-15. Paratype. NMB No. H 10539. Height 25.0 mm, diameter 6.9 mm. Chaussy, NW of Paris, France, Lutetian; 3 ×.

16-18. Holotype. NMB No. H 14491. Height 22.7 mm, diameter 6.3 mm. Chaussy, NW of Paris, France, Lutetian; 3 ×.

## EXPLANATION OF PLATE 11

*Figure* *Page*

1-6. *Paraseraphs* cf. *armoricensis* (Cossmann) ........ 37

1-2. NMB No. H 16559. Artificial cast of U.S. Nat. Mus., No. 135097. Height 56.9 mm, diameter 11.6 mm. Near Port Antonio, Portland, Jamaica, probably late Eocene; 2 ×.

3-4. NMB No. H 16558. Artificial cast of U.S. Nat. Mus., No. 135097. Height 44.6 mm, diameter 10.5 mm. Near Port Antonio, Portland, Jamaica, probably late Eocene; 2 ×.

5-6. NMB No. H 16560. Artificial cast of U.S. Nat. Mus., No. 135097. Height 47.2 mm, diameter 12.1 mm. Near Port Antonio, Portland, Jamaica, probably late Eocene; 2 ×.

7-15. *Paraseraphs propedistortus* (de Gregorio) ........ 38

7-8. NMB No. H 14510. Height 31.0 mm, diameter 7.9 mm. Piana-Cornedo, west of Schio, northern Italy, Lutetian; 2 ×.

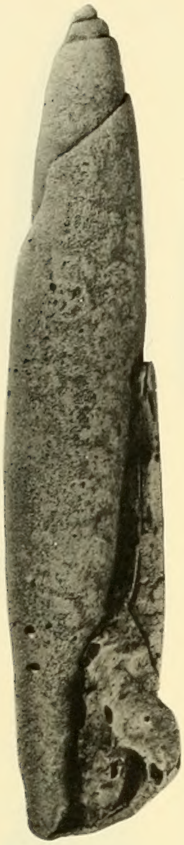
9-11. NMB No. H 16503. Height 23.6 mm, diameter 7.8 mm. Ciuppo near San Giovanni Ilarione, northern Italy, Lutetian; 2 ×.

12-13. NMB No. H 14509. Height 53.2 mm, diameter 11.4 mm. Piana-Cornedo, west of Schio, northern Italy, Lutetian; 2 ×.

14-15. NMB No. H 16501. Height 55 mm (estimated), diameter 11.9 mm. Piana, west of Schio, northern Italy, Lutetian; 2 ×.

16.17. *Paraseraphs propedistortus* (de Gregorio) ? ........ 39

NMB No. H 14546. Height 46.1 mm, diameter 9.7 mm. Mokattam near Cairo, Egypt, Lutetian; 2 ×.



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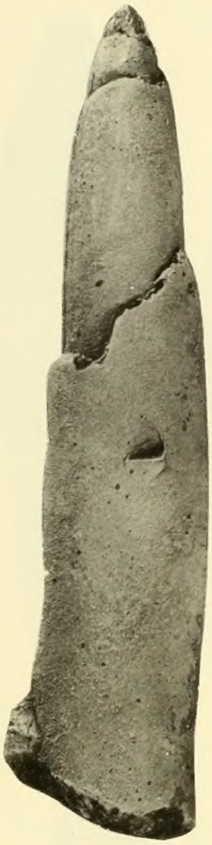

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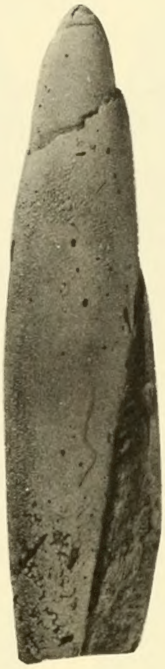

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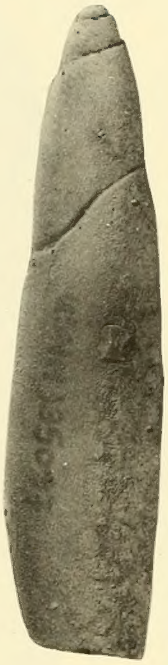

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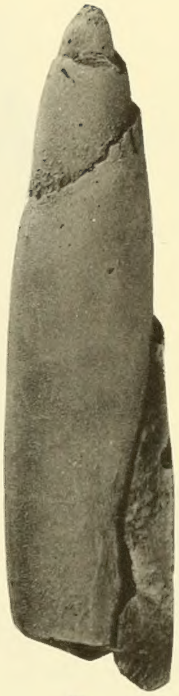

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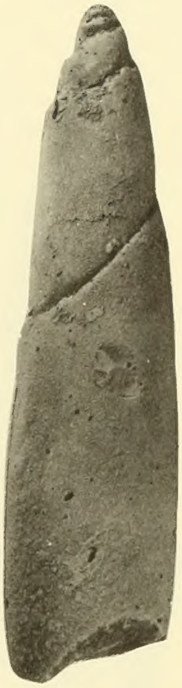

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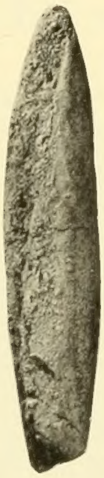

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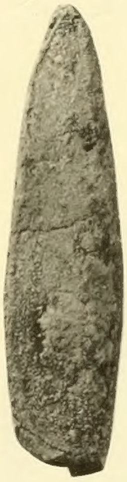

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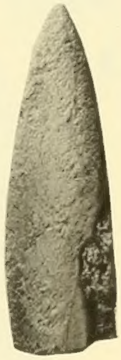

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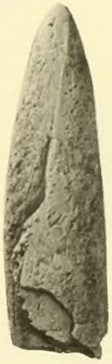

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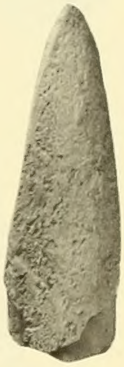

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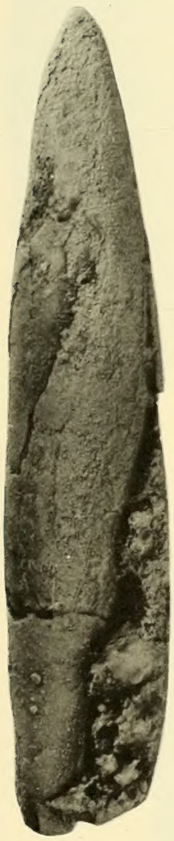

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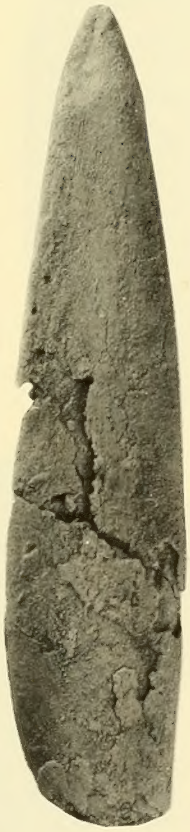

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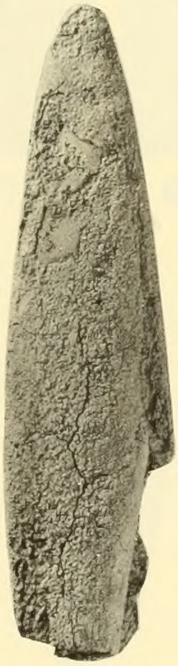

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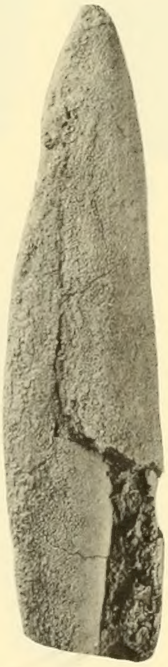

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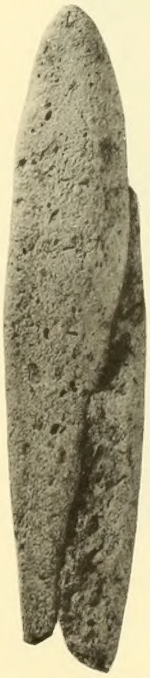

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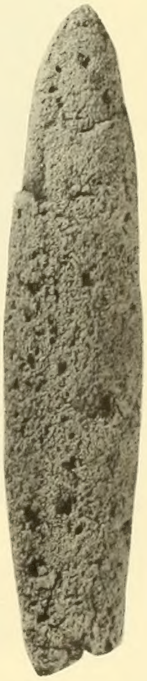

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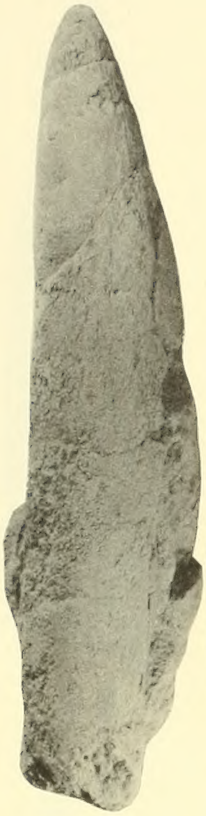
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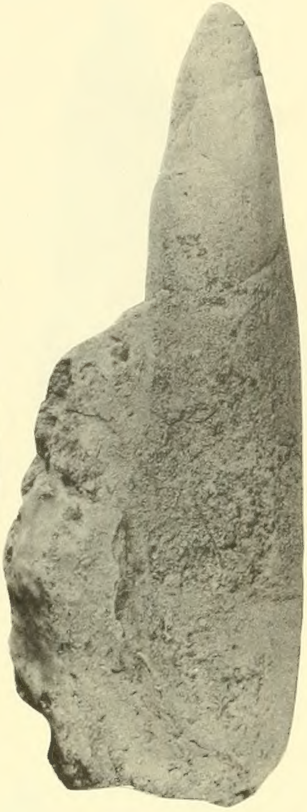
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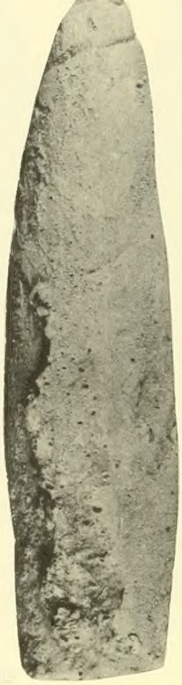
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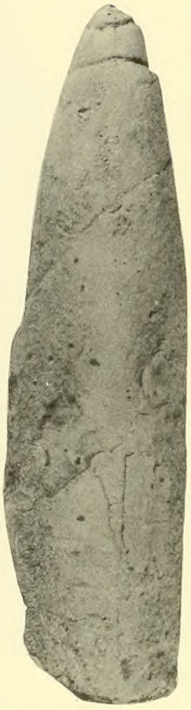
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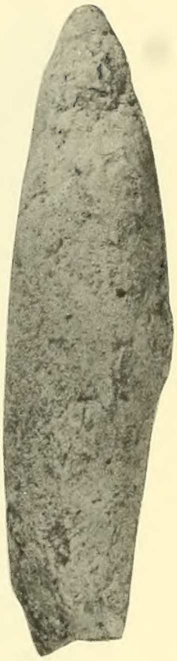
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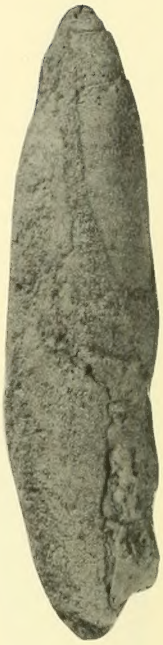
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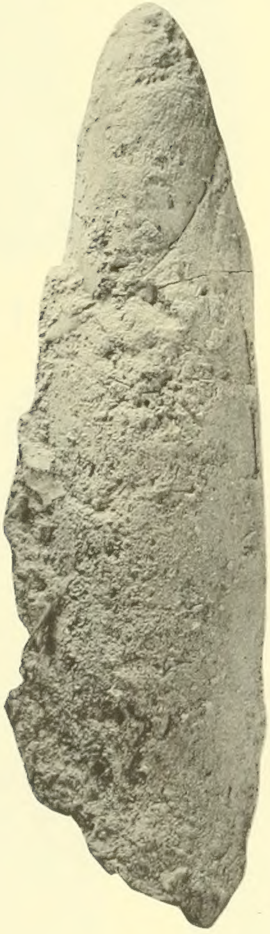
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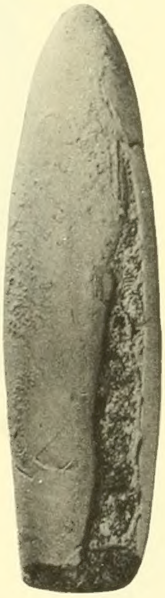
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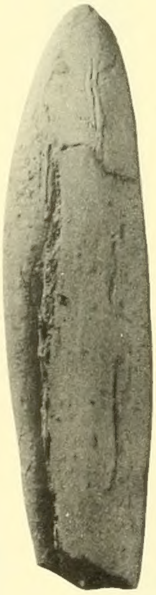
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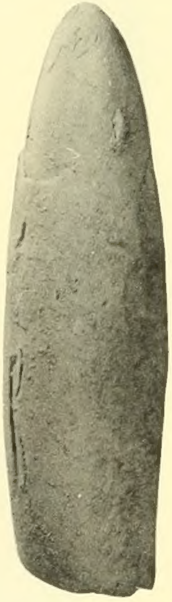
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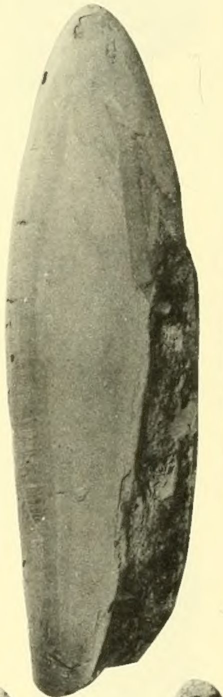
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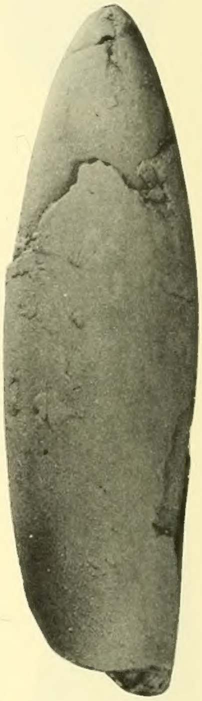
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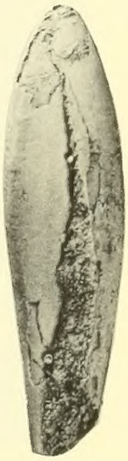
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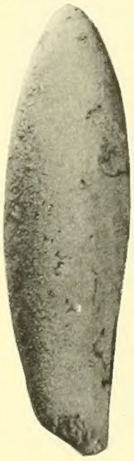
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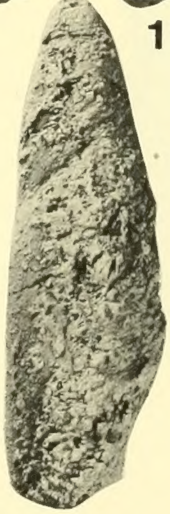
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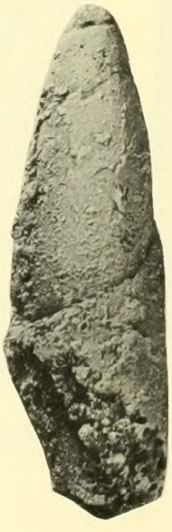
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## EXPLANATION OF PLATE 12

| *Figure* | | *Page* |
|---|---|---|
| 1-7. | *Paraseraphs procerus* (Merian) | 39 |
| | 1-2. Holotype. NMB No. H 14374. Height 71.8 mm, diameter 16.4 mm. Jamaica (exact locality not known), middle Eocene; 1.5 ×. | |
| | 3-4. NMB No. H 16564. Artificial cast of U.S. Nat. Mus., No. 645055. Height 62.0 mm, diameter 16.5 mm. Spring Mount, St. James, Jamaica, middle Eocene; 1.5 ×. | |
| | 5-6. NMB No. H 16563. Height 57.3 mm, diameter 14.6 mm. Spring Mount, St. James, Jamaica, middle Eocene; 1.5 ×. | |
| | 7. Lectotype of *Terebellum subdistortum* Trechmann. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. GG 5471. Specimen figured by Trechmann (1923, pl. 18, fig. 8). Spring Mount, St. James, Jamaica, middle Eocene. Photograph courtesy British Museum (Natural History); 1.5 ×. | |
| 8-14. | *Paraseraphs erraticus* (Cooper) | 41 |
| | 8-10. NMB No. H 16551, Artificial cast of holotype of *Terebellum californicum* Vokes, University of California, Museum of Paleont., No. 15820. Height 26.8 mm, diameter 7.9 mm. UC-locality A-976, Domengine, Fresno County, California, late (?) Eocene; 3 ×. | |
| | 11-12. NMB No. H 16553. Artificial cast of paratype of *Terebellum californicum* Vokes, Univ. California, Museum of Paleont., No. 15822. Height 31.4 mm, diameter 9.0 mm. UC-locality 3296, east of Simi Valley, California, late (?) Eocene; 3 ×. | |
| | 13-14. NMB No. H 16552. Artificial cast of paratype of *Terebellum californicum* Vokes, Univ. California, Museum of Paleont., No. 15821. Height 20.6 mm, diameter 5.8 mm. UC-locality A-1164, Garza Creek, California, late (?) Eocene; 3 ×. | |
| 15-16. | *Paraseraphs* aff. *erraticus* (Cooper) | 41 |
| | NMB No. H 14470. Height 23.0 mm, diameter 7.0 mm. Soldado Rock, Trinidad, Boca de Serpiente formation (middle Eocene); 3 ×. | |

## EXPLANATION OF PLATE 13

*Figure* *Page*

1-3. *Paraseraphs erraticus* (Cooper) ........ 41

1. Holotype. California Academy of Sciences, No. 608. Height 19.3 mm, diameter 6.4 mm. Rose Cañon, San Diego County, California, Cretaceous B (= Eocene). Front view. Photograph courtesy California Academy of Sciences; about 2 ×.

2-3. NMB No. H 16550. Artificial cast of holotype of *Tornatina erratica* Cooper. Side and rear views; 3 ×.

4-6. *Terebellum cinctum* Martin ........ 42

Holotype. Rijksmuseum van Geologie en Mineralogie, Leiden, No. St. 10337. Height 34.7 mm, diameter 10.3 mm. Kembang Sokkoh, West Progo Mountains, Java, "early Miocene". Photograph courtesy Rijksmuseum van Geologie en Mineralogie, Leiden; 2 ×.

7-11. *Terebellum papilliferum* Martin ........ 43

7-8. NMB No. H 14468. Height 32.6 mm, diameter 10.3 mm. Gunung Spolong, West Progo Mountains, Java: "early Miocene"; 2 ×.

9-11. Lectotype. Rijksmuseum van Geologie en Mineralogie, Leiden, No. St. 10339. Height 28.0 mm, diameter 8.3 mm. Gunung Spolong, West Progo Mountains, Java, "early Miocene". Photograph courtesy Rijksmuseum van Geologie en Mineralogie, Leiden; 2 ×.

12-18. *Terebellum obtusum* J. de C. Sowerby ........ 43

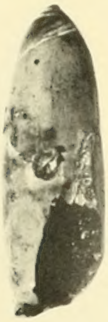
12-14. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. GG 21008. Height 29.1 mm, diameter 12.1 mm. Specimen figured by d'Archiac and Haime (1854, pl. 32, fig. 21). Sind, Gaj beds (middle Miocene); 2 ×.

15-16. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. G 50793. Height 44.2 mm, diameter 11.2 mm. Soomrow, Cutch, NW India, Gaj beds (middle Miocene); 2 ×.

17-18. Holotype. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. GG 21000. Height 42.2 mm, diameter 13.5 mm. Soomrow, Cutch, NW India, Gaj beds (middle Miocene); 2 ×.

19-20. *Paraseraphs* sp. ........ 39

NMB No. H 16592. Artificial cast of U.S. Nat. Mus., No. 645463. Height 40.7 mm, diameter 13.0 mm. Maraguán road, 15 miles east of Camaguey, Cuba, unspecified Eocene horizon; 1.5 ×.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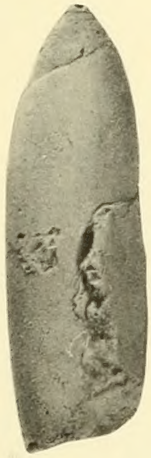
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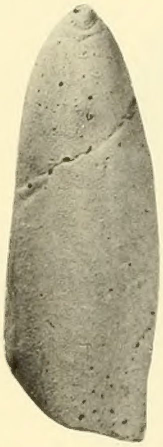
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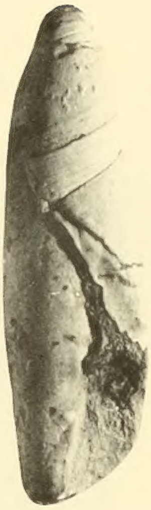
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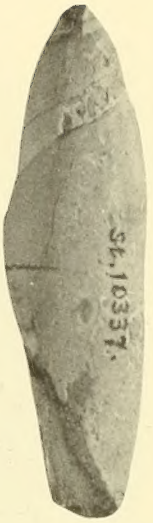

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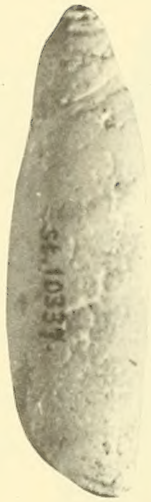

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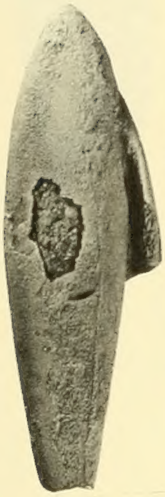
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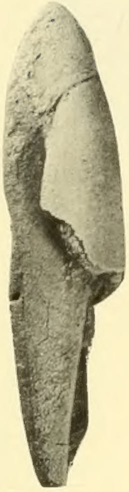
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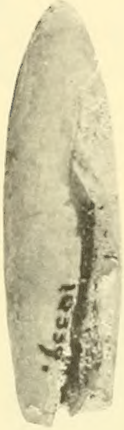
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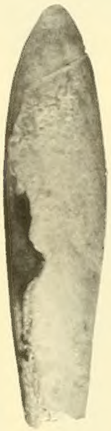
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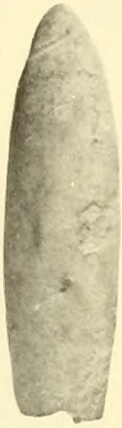
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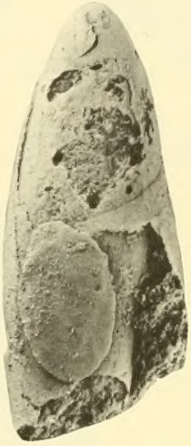
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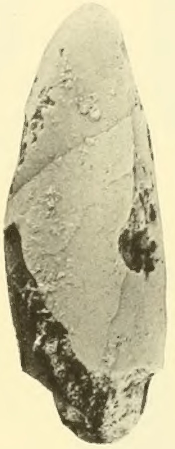
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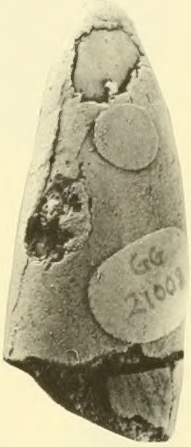

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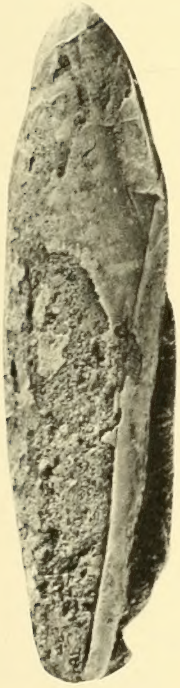
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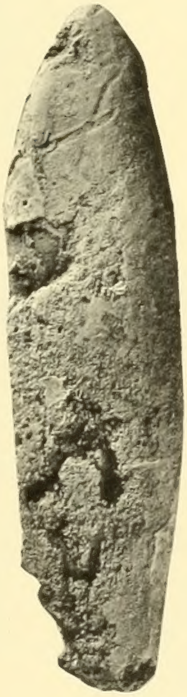
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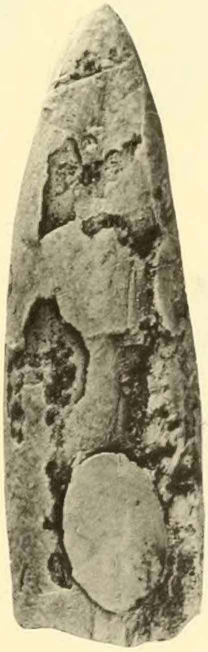
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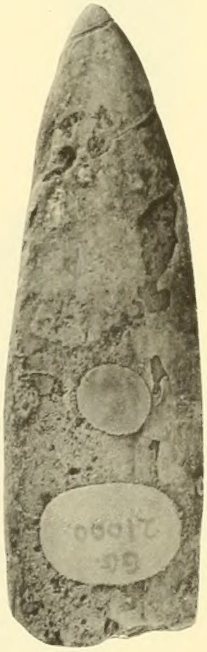
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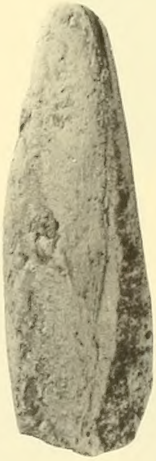
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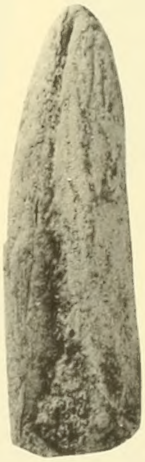
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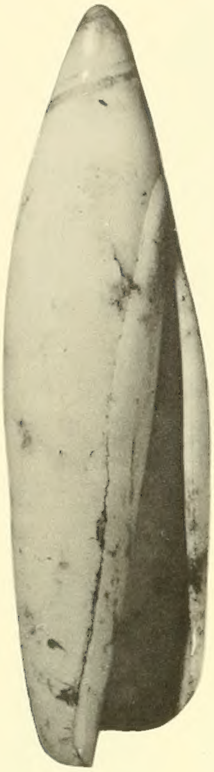
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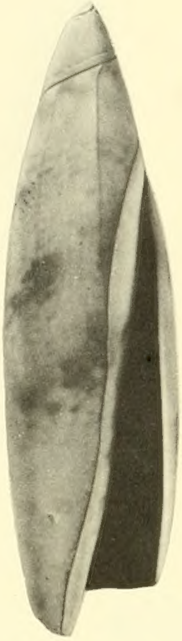
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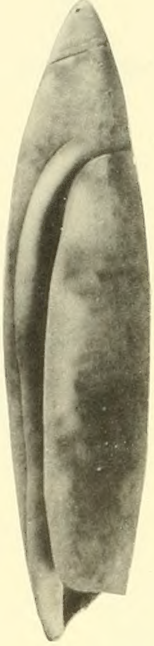
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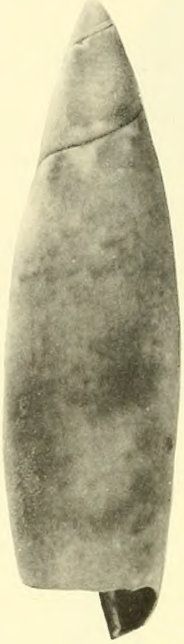
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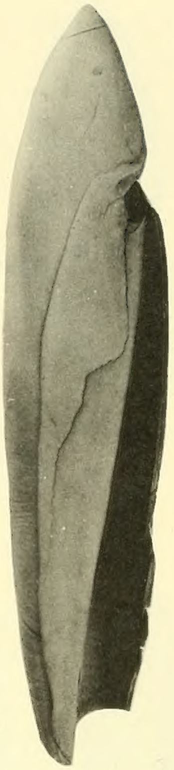
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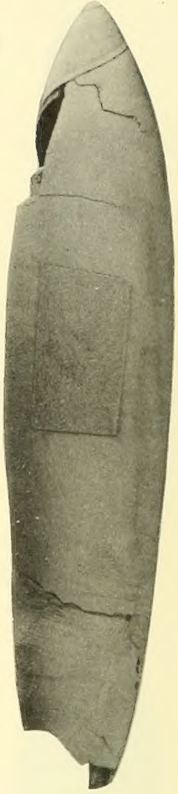
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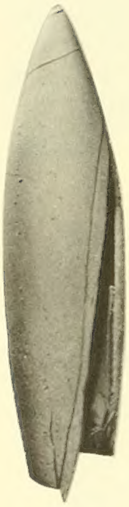
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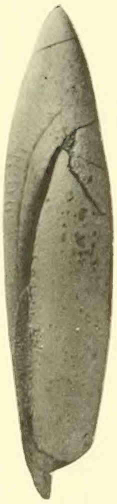
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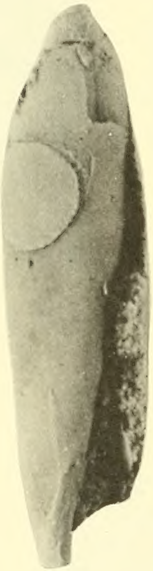
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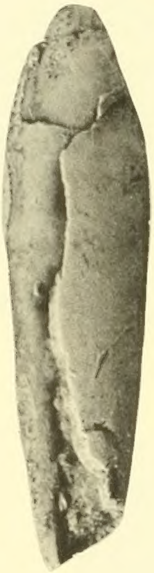
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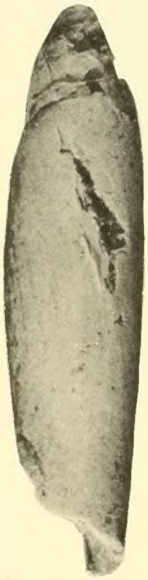
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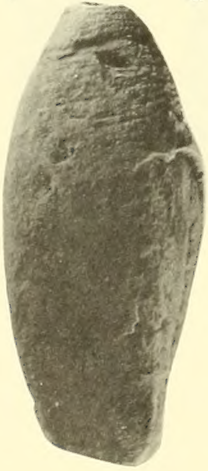
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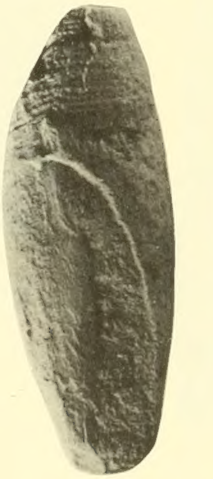
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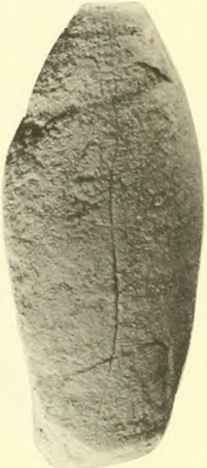
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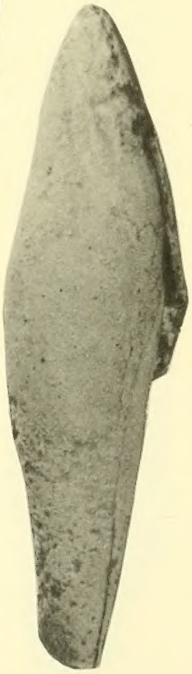
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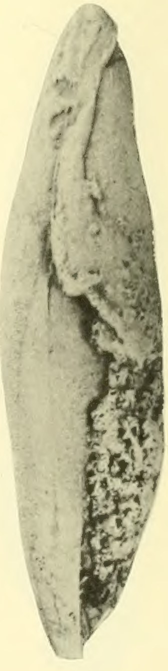
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## EXPLANATION OF PLATE 14

*Figure* *Page*

1-8. *Terebellum terebellum* (Linné) ........ 44

1. Lectotype. Linnean collection, at present at the British Museum (Natural History). Height 37.5 mm, diameter 10.6 mm. Recent. No locality information; 3 ×.

2-4. NMB No. H 16599. Height 28.3 mm, diameter 7.7 mm. Recent. Salomon Islands. Same specimen as that shown in Text-figure 13; 3 ×.

5-6. NMB No. H 14471. Height 50.7 mm, diameter 11.4 mm. Menubar, Sankulirang, North Kutei, Borneo: Pliocene; 2 ×.

7-8. NMB No. H 14469. Height 33.1 mm, diameter 8.5 mm. Below Kailoefak, Wai Beli, East Ceram, Pliocene; 2 ×.

9-11. *Terebellum* sp. ........ 44

Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. G 54486. Height 17.4 mm. Island of Nias, off Sumatra, "Miocene". Specimen figured by Woodward (1879, pl. 13, fig. 6).

12-14. *Terebellum diversiornatum* Eames ........ 44

Holotype. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. G 68239. Height 10.1 mm, diameter 4.5 mm. Zinda Pir, West Punjab, Pakistan, early Eocene; 6 ×.

15-16. *Paraseraphs* ? sp. ........ 47

NMB No. H 16593. Artificial cast of U.S. Nat. Mus., 645468. Height 60.2 mm, diameter 16.8 mm. Jhirak, Sind, Pakistan, probably upper Ranikot beds (late Paleocene); 1.5 ×.

## EXPLANATION OF PLATE 15

*Figure* *Page*

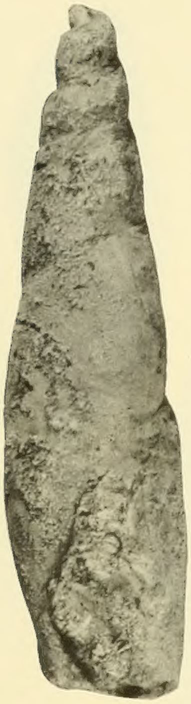
1-3. *Tibia (Terebellopsis) brauni* (Leymerie) ........ 46
Leymerie Collection, Natural History Museum, Toulouse, France, unnumbered. Height 61.8 mm, diameter 16.6 mm. Montolieu, Montagne Noire, southern France, late Paleocene; 1.5 ×.

4-6. *Tibia (Terebellopsis)* cf. *brauni* (Leymerie) ........ 47
NMB No. H 16575. Height 74.0 mm, diameter 16.2 mm. Simpheropol, Crimea, USSR, possibly Lutetian; 1.5 ×.

7-12. *Tibia ? (Terebellopsis ?) distorta* (d'Archiac and Haime) ........ 48
7-9. Syntype. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. GG 21005. Height 41.2 mm, diameter 13.0 mm. Ranikot, Sind, Pakistan, late Paleocene. Specimen figured by d'Archiac and Haime (1854, pl. 32, fig. 19); 2 ×.

10-12. Syntype. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. GG 21006. Height 37.9 mm, diameter 13.3 mm. Ranikot, Sind, Pakistan, late Paleocene. Specimen figured by d'Archiac and Haime (1854, pl. 32, fig. 19a); 2 ×.

13-15. *Tibia (Semiterebellum) marceauxi* (Deshayes) ........ 46
Muséum National d'Histoire Naturelle, Paris, No. B 63189. Height 73.4 mm, diameter 26.1 mm. Jonchery-sur-Vesle, Dept. Marne, France, Thanetian (Paleocene); 1.5 ×.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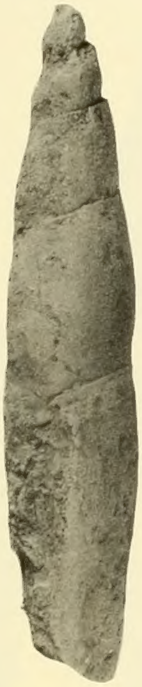
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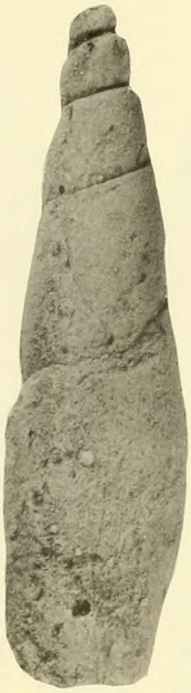
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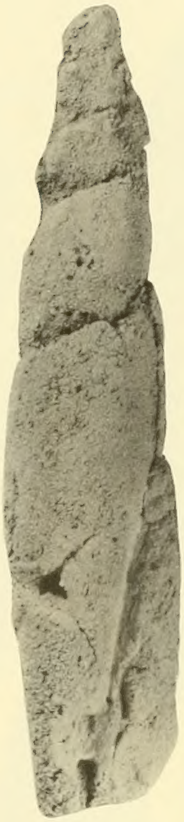
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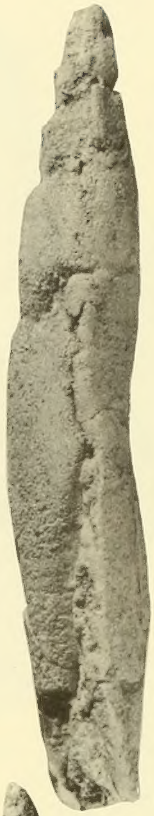
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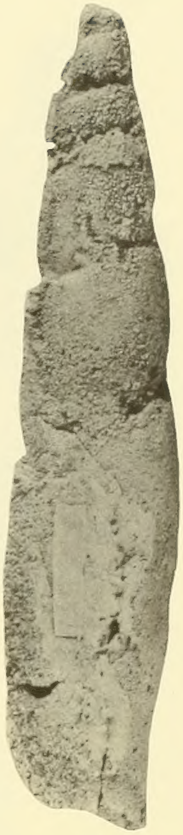
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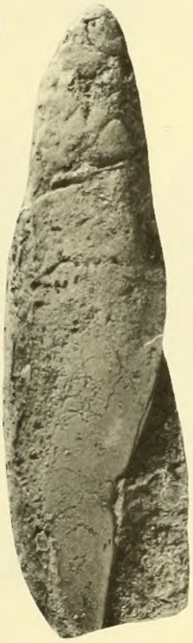
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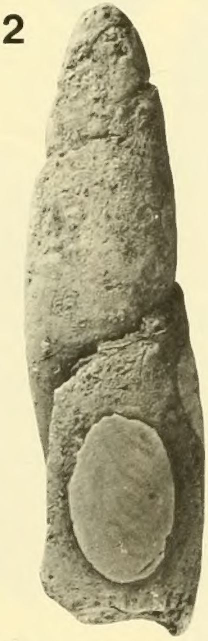
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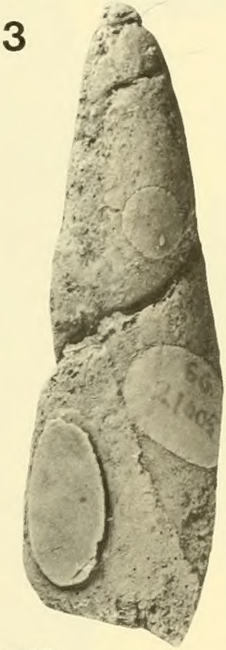
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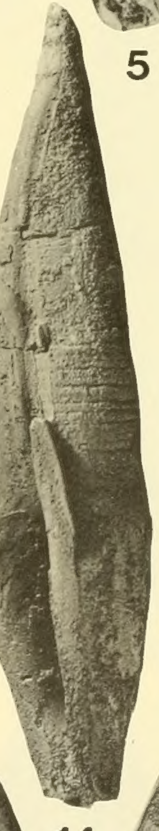
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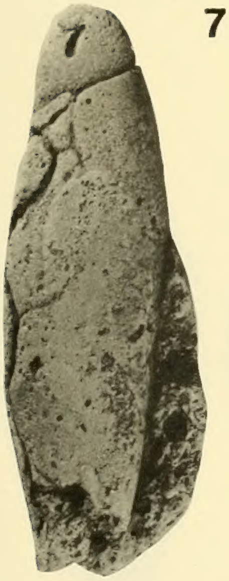
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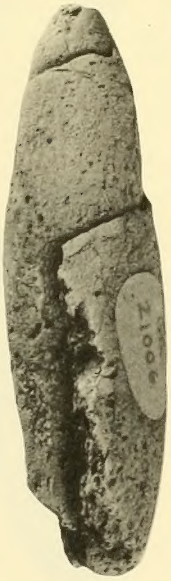
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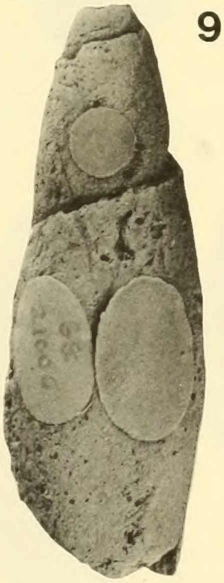
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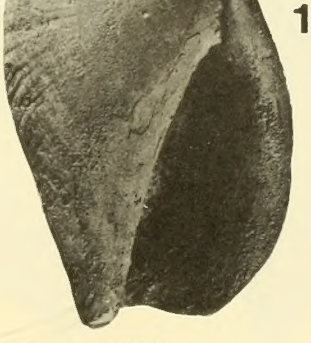
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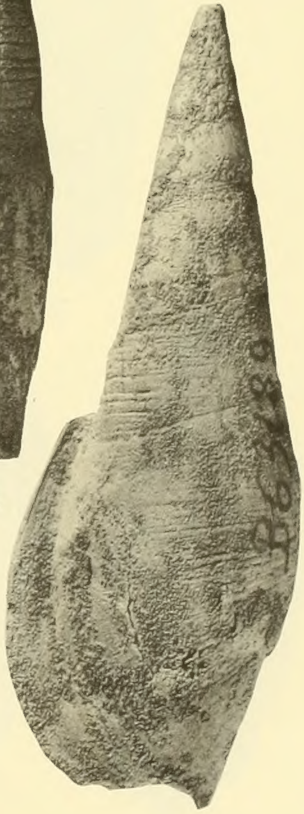
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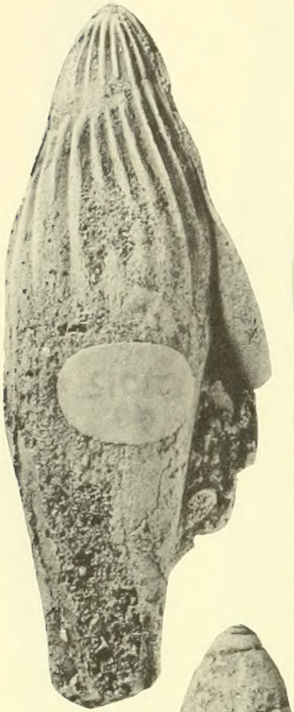
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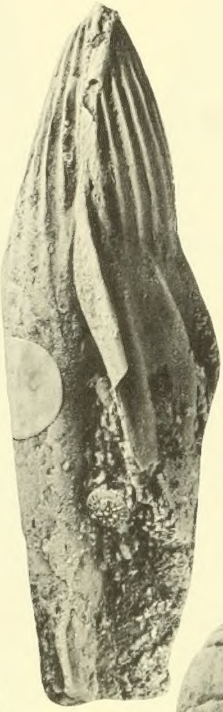
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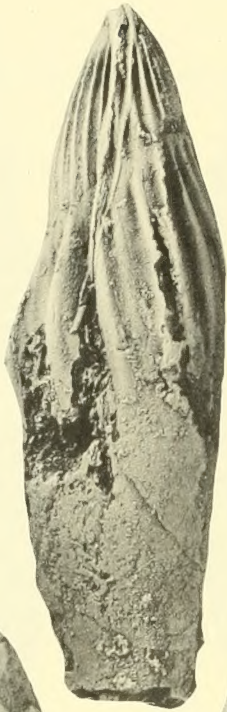
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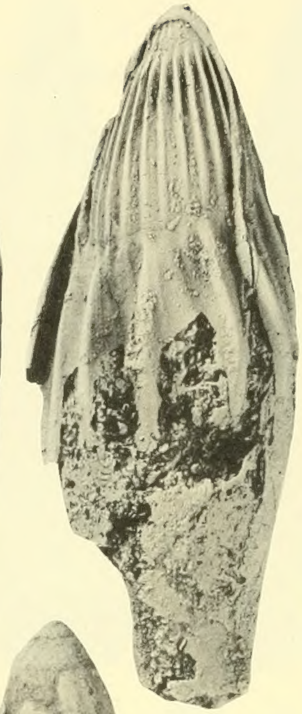
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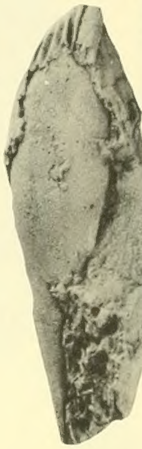
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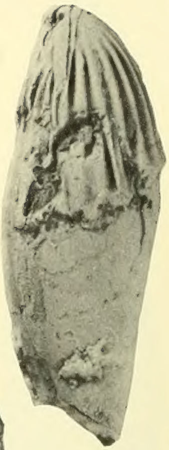
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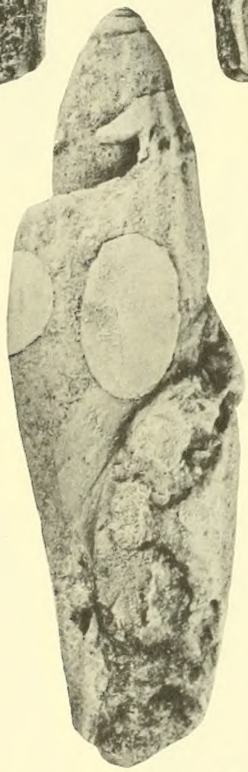
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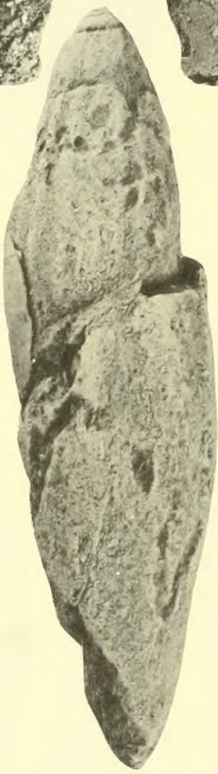
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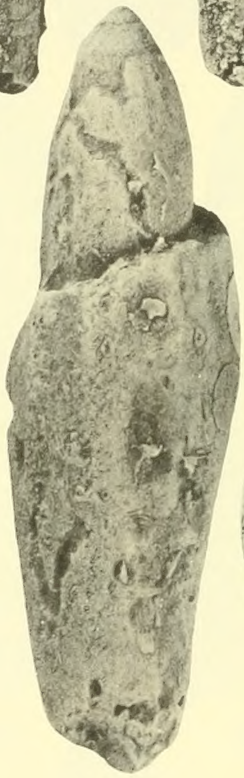
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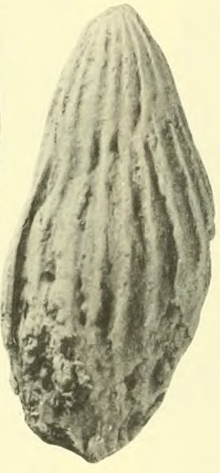
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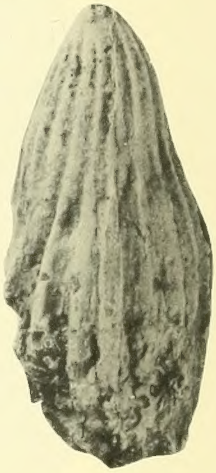
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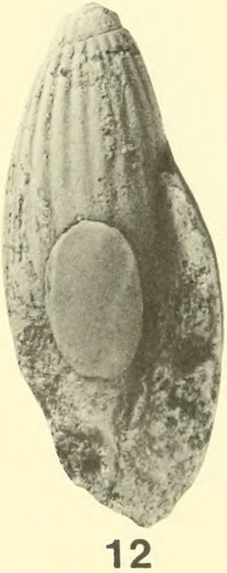
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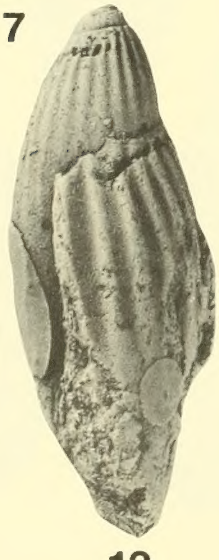
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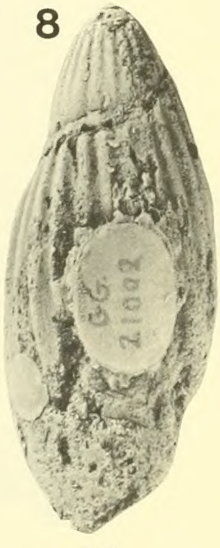
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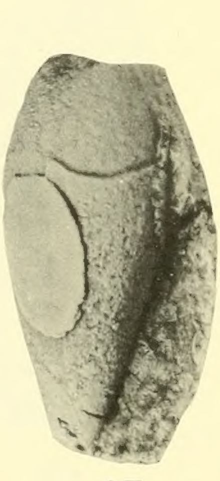
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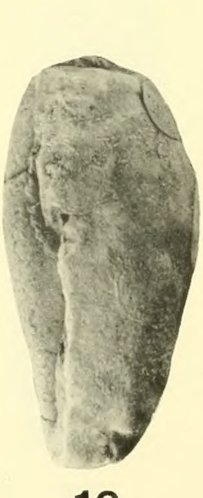
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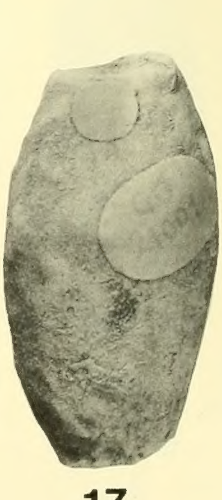
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## EXPLANATION OF PLATE 16

*Figure* *Page*

1-14. *Mauryna plicata* (d'Archiac and Haime) .......... 48

1-4. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. GG 21015. Height 46.5 mm, diameter 17.2 mm. Unspecified locality in Sind, Pakistan, upper Ranikot beds (late Paleocene); 2 ×.

5-6. NMB No. H 16569. Artificial cast of U.S. Nat. Mus., No. 645467. Height 30.0 mm, diameter 11.0 mm. Jhirak, Sind, Pakistan, upper Ranikot beds (late Paleocene); 2 ×.

7-9. Paralectotype. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. GG 21003. Height 50.0 mm, diameter 14.3 mm. Ranikot, Sind, Pakistan, upper Ranikot beds (late Paleocene). Specimen figured by d'Archiac and Haime (1854, pl. 32, fig. 18); 2 ×.

10-11. NMB No. H 16568. Artificial cast of U.S. Nat. Mus., No. 645467. Height 31.1 mm, diameter 14.8 mm. Jhirak, Sind, Pakistan, upper Ranikot beds (late Paleocene); 2 ×.

12-14. Lectotype. Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. GG 21002. Height 35.2 mm, diameter 14.1 mm. Ranikot, Sind, Pakistan, upper Ranikot beds (late Paleocene). Specimen figured by d'Archiac and Haime (1854, pl. 32, fig. 17); 2 ×.

15-17. *Seraphs (Seraphs) sopitus* (Solander) ? .......... 49

Brit. Mus. (Nat. Hist.), Dept. Palaeont., No. GG 21004. Height 26.4 mm, diameter 13.6 mm. Salt Range, India, Laki beds (early Eocene). Specimen figured by d'Archiac and Haime (1854, pl. 32, fig. 22) as *Terebellum plicatum* and re-identified by Cox (1931b, pp. 51-52) as *Terebellum carcassense* Leymerie ? 2 ×.

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# ANATOMY AND MORPHOLOGY OF PSILOPHYTON DAWSONII, SP. N. FROM THE LATE LOWER DEVONIAN OF QUEBEC (GASPÉ), AND ONTARIO, CANADA

By

H. P. BANKS, SUZANNE LECLERCQ, AND F. M. HUEBER

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(Founded 1917)

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April 7, 1975

Paleontological Research Institution
Ithaca, New York, U.S.A. 14850

*Library of Congress Card Number: 75-8034*

Printed in the United States of America
Arnold Printing Corporation

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# ANATOMY AND MORPHOLOGY OF *PSILOPHYTON DAWSONII,* SP. N. FROM THE LATE LOWER DEVONIAN OF QUEBEC (GASPÉ) AND ONTARIO, CANADA

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## ABSTRACT

For the first time a species of *Psilophyton* is described from petrifactions. The specimens come from Early Devonian (Emsian) calcareous cobbles on the Gaspé Peninsula near Douglastown, P. Q., Canada. Compression specimens, occasionally petrified by iron pyrite, from along Abitibi River near Coral Rapids, James Bay Lowlands, Ontario, Canada, show identical anatomy and morphology. Epidermis, stomata, thick- and thin-walled cortical cells, phloem, and a centrarch xylem strand are recorded for branches of several orders; details of branch traces and of dichotomies in lesser axes are reported. Larger axes bear closely and spirally arranged vegetative branches in zones alternating with spirally arranged but alternate and distichous fertile branch systems. The latter usually branch six times and are three-dimensional because successive dichotomies occur 90° around the stem from one another. Each of the first two apparent dichotomies is two close divisions which would result in three axes. However one of the three aborts. This leaves an apparent dichotomy with a strange stump near its axil. The ultimate fertile branches terminate in fusiform sporangia whose walls resemble epidermal and cortical cells of the axes. Vascular tissue extends into the base of the sporangia. A thin membrane surrounds the mass of isospores which resemble most closely the spore-genus *Retusotriletes.* Dehiscence of sporangia is longitudinal along one side.

The vascular strand is terete, has one central protoxylem when not branching, and is massive compared to that of *Rhynia.* Annular and spiral elements occur in the protoxylem and scalariform elements in the metaxylem. The latter are characteristic because interconnections between the scalariform bars, formed by secondary wall material, outline thin areas of wall that thus simulate pits. The vascular strand is large and complex in the area of profuse vegetative branching and the traces to fertile branch systems are distinctively rectangular strands in transverse section. No leaves are present but some of the smaller vegetative branch systems as well as lesser laterals on some of the stemlike branch systems could be interpreted as precursors of leaves. The height of the plant and its base are unknown.

*Psilophyton dawsonii,* n. sp. is placed in the Trimerophytina and represents anatomically and morphologically the best known species in the subdivision. It is considered to be far more highly evolved than *Rhynia* and adds significant details for use in analysis of the plexus from which younger groups such as the coenopterids and progymnosperms could have evolved.

## INTRODUCTION

The generic name *Psilophyton* and all the concepts that it connotes came to be almost synonymous with Devonian Flora and the origin of land plants. *Psilophyton* has been used as the type of several taxonomic categories, *e.g.* Psilophytales. It has given substance to hypotheses widely used in morphology, *e.g.* the telom theory of Zimmermann (1930). Yet, until 1967 (Hueber and Banks, 1967) its principal species, *P. princeps,* was not represented by a type specimen, several different kinds of axes were attributed to the species, and the connection of sporangia to larger axes was uncertain. Similarly there was no useful information concerning its anatomical structure. In 1968 Hueber described *P. princeps* in some detail and the present material permits us to describe a new species for which we can combine in one account the details of both its gross morphology and its anatomical structure. Hueber's work and our new, extensive discoveries should remove any remaining doubt as to the exact vascular structure and the morphological complexity of this historic genus.

All types are on deposit at Cornell University Paleobotanical Collection (CUPC), Geological Survey of Canada (GSC) and National Museum of Natural History (U.S. Nat. Mus.).

## ACKNOWLEDGMENTS

We wish to thank Dr. D. C. McGregor of the Geological Survey of Canada for analyzing the spore content of our specimens in order to determine the stratigraphic level of our plants within the Battery Point Formation, Dr. M. Streel (Liège) for help in the interpretation of the spores of *P. dawsonii,* M. Discry and M. Lhode (Liège) for technical assistance, Jane Blanchard (Cornell University) for her interest and skill in the production of the photographs, and Sonia Kossow Guterman for exploiting the technique of demineralizing petrifactions, embedding them in paraffin and microtoming. Special thanks go to Elfriede Abbe for her rendering of the reconstruction of the new plant.

We thank the former Director of the Section of Paleobotany Dr. Olaf Selling, Swedish Museum of Natural History, who loaned, early in our study, specimens described by Halle on which we were able to demonstrate aborted branches; Dr. John Pettitt, British Museum (Natural History), for assistance in the study of materials and preparations described by Croft and Lang and for his preparation of membranes isolated from sporangia described here from Gaspé; Dr. V. Zazvorka, Head Curator, Department of Paleontology, at the National Museum at Prague, Czechoslovakia, for assistance in the study of Bohemian *Psilophyton;* Dr. F. Stockmans for many courtesies during the study of his collections at Institut Royal des Sciences Naturelles de Belgique, Brussels; Dr. O. A. Høeg for advice and assistance during the study of his extensive collections at the University of Oslo; Alice Johansson, Director at the time of our studies and Louise Stevenson, Curator of Geology, for the opportunity to work extensively with the Dawson Collection at the Redpath Museum, McGill University.

We also thank the Geological Survey of Canada for permission to study and describe the specimens collected along the Abitibi River, Ontario.

The research of Banks has been supported by a J. S. Guggenheim Memorial Foundation Fellowship, by Federal Hatch Funds, and by National Science Foundation Grants GB-4993 and GB-8282X. These have permitted a semester at University of Liège with Leclercq to reconstruct the plant from peels and visits to study appropriate specimens in the Halle Collection in the Section for Paleobotany of the Swedish Museum of Natural History, in the Lang and the Croft and Lang Collections of the Department of Paleontology, British Museum (N.H.), in the Dawson Collection of the Redpath Museum, McGill University, in the Stockmans Collection of the Institut Royal des Sciences Naturelles de Belgique, Brussels, in the Department of Paleontology, National Museum of Prague, and in the Geological Museum of the University of Oslo.

Leclercq wishes to express her thanks to Cornell University for her appointment as Visiting Professor for three months in 1963. This permitted her to begin the study of the anatomy of *Psilophyton dawsonii*, n. sp., as revealed in serial peels of calcareous cobbles from the Gaspé Bay area and to carry on the study at the University of Liège.

The research of Hueber has been supported by funds from the Roland W. Brown Fund for paleobotanical research and the Smithsonian Research Foundation. Both have made possible the payment of travel expenses to study collections at the Redpath Museum, McGill University, the British Museum (Natural History), Institut Royal des Sciences Naturelles de Belgique, Brussels, the University of Oslo, and the Swedish Museum of Natural History, Stockholm.

## HISTORICAL SURVEY

The genus *Psilophyton* was erected by Dawson in 1859 for Devonian fossils found on the Gaspé Peninsula, Quebec, Canada. He described two species, *P. princeps* and *P. robustius*. The latter has proved to be different. It is now in part *Trimerophyton robustius* Hopping (1956). In 1871 Dawson described a new variety which he named *P. princeps* var. *ornatum* (now *Sawdonia ornata* (Dn.), Hueber, 1971, a member of Zosterophyllophytina Banks, 1968, and no longer a psilophyte). These specimens of 1871 came gradually and informally to represent the type of the species *P. princeps*. Four arguments supported this interpretation. First, Dawson's original description and restoration (Text-fig. 1) united diverse organs without proof of their organic connection. Second, in 1871 Dawson provided satisfactory illustrations of spine-bearing axes, and he had originally described *P. princeps* as spiny. Third, in 1871 Dawson described terminal sporangia of *Psilophyton* which were well enough preserved to be accepted as sporangia by most workers although they were *not* attached to the new large spiny axes. Fourth, in 1870 Dawson had published a new, more reasonable, reconstruction of *P. princeps* (Text-fig. 2) which has been copied by many subsequent authors.

In 1895 Solms-Laubach analyzed critically the then current status of studies on *Psilophyton*. He pointed out that neither the fructifications described in 1859 nor those of 1871 were attached to spiny stems. He noted also that the few anatomical details Dawson had recorded for the stems came from unattached fragments and should not be regarded as belonging to *Psilophyton*.

In 1905 White studied the Upper Devonian flora of Perry, Maine, and also some of Dawson's collection from the Gaspé Peninsula (Lower Devonian). He concluded that the spiny stems described and illustrated as *Psilophyton princeps* var. *ornatum* (Dawson, 1871, pl. 9, figs. 97-101) should be regarded as the type of *P. princeps*. He examined the unattached fructifications decribed by Dawson (1871, pl. 9, figs. 102, 103, 105-108) and found punctate areas on the sporangium-bearing axes. These impressed White as representing the bases of spines. Therefore, unlike Solms-Laubach, he united the terminal sporangia Dawson (1871) described as "Fructifications consisting of naked, oval spore-cases borne usually in pairs on slender curved pedicels, either lateral or terminal" with the spiny axes. That is to say he united all the organs illustrated by Dawson on plate 9, 1871, under the epithet *P. princeps* var. *ornatum*. Dawson believed the fertile axes belonged to his original *P. princeps*. White's suggestion, followed by many subsequent workers, meant the elimination of the variety *P. princeps* var. *ornatum* and the definition of *P. princeps* as a plant with numerous large spines rather than the slender, distant ones described originally in 1859 by Dawson. We shall show subsequently that White had good reason to believe that *P. princeps* bore both spines and paired terminal sporangia. The evidence will show, however, that he was not correct in associating the paired terminal sporangia with the stems Dawson had named *P. princeps* var. *ornatum*.

Halle (1916) continued the analysis of *Psilophyton* with a careful study of poorly preserved fossils collected in Lower Devonian strata at Röragen, Norway. Like Solms-Laubach he rejected Dawson's description of anatomy because the partially petrified specimens were not parts of spiny stems. For the same reason he rejected the unattached organs that Dawson had called rhizomes. We found three specimens labeled rhizome of *Psilophyton* by Dawson. These bear numbers 3203, 3205, 3206 in the Redpath Museum, McGill University. They are not connected to any axes of *Psilophyton* but they do have all the characteristics of *Taeniocrada dubia*. The late Dr. Kräusel, who also studied Dawson's collections, as well as European materials, agreed in 1959 at X International Botanical Congress, Montreal, that Dawson's rhizomes should be referred to *T. dubia*. Halle also rejected the paired, terminal sporangia on the ground that one must find actual spines on the reproductive

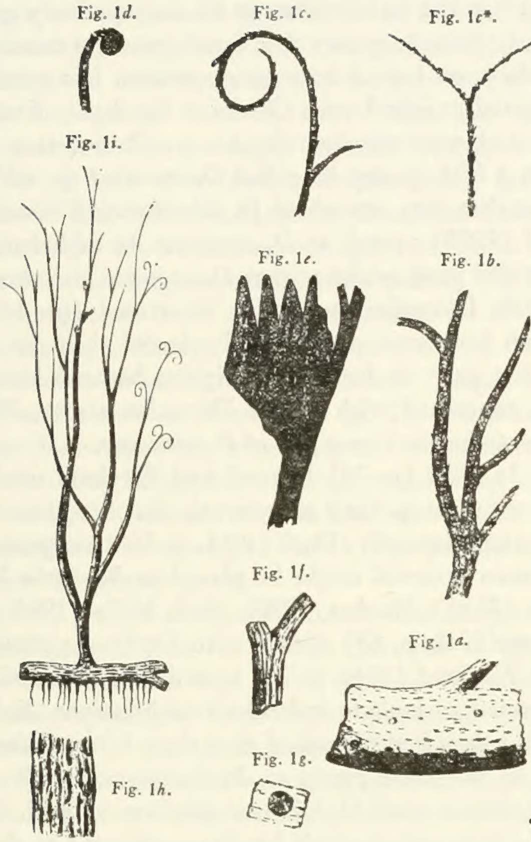
Fig. 1d.
Fig. 1c.
Fig. 1c*.
Fig. 1i.
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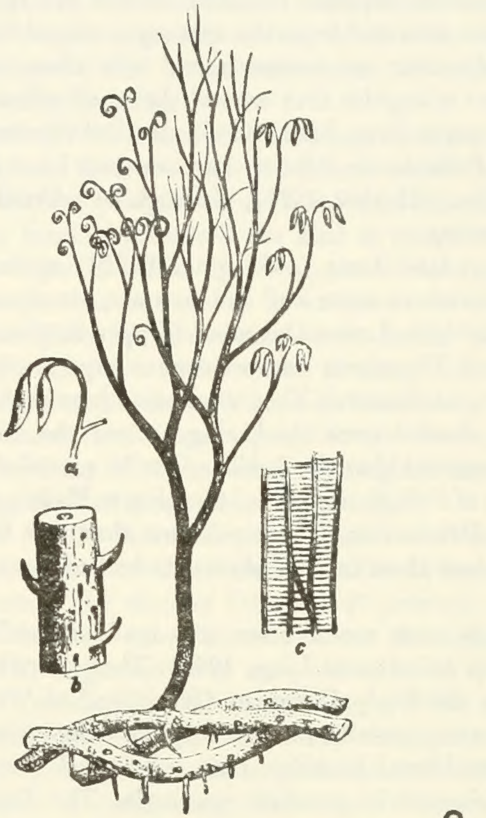

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Text-figures 1, 2. — Text-figure 1 (left) Dawson's original drawings and reconstruction of *Psilophyton princeps*, 1859. Text-figure 2 (right) Dawson's revised reconstruction of *P. princeps* first published in 1870.

axes, not simply scars of spines. Thus, following Halle's paper, *Psilophyton princeps* was reduced to a spiny, vegetative axis that branched dichotomously.

Halle was constructive in his analysis. He compared the Röragen material with some specimens from the Gaspé Peninsula and concluded that Dawson's fertile axes bearing terminal sporangia (*e.g.* Dawson 1871, pl. 9, fig. 102) had no spines and were striated vertically whereas the axes of *Psilophyton* were unstriated and spiny. Halle, therefore, erected a "provisional" category, *Dawsonites arcuatus,* for the reception of axes from Gaspé, Röragen, and Matringhem, France (Bertrand 1913), that bore narrow obovoid, or short-fusiform, terminal sporangia, usually 3 to 5 mm in length, on slender, curved branches. The ultimate branches terminated a system of bifurcating lateral branches. Even more important was Halle's perceptive and convincing argument that these fertile axes foreshadowed the morphological pattern found among early preferns.

In 1931 Lang began to contribute to this problem with his usual care and skill. First, he studied specimens from the Gaspé Peninsula which had been labeled *Psilophyton princeps*. Among the material he found some axes with longitudinal ridges (like *Dawsonites*) and occasional spines (like *Psilophyton*) that seemed to bear terminal sporangia (like *Dawsonites*). Lang considered these specimens to be identical to Halle's *Dawsonites* but he called them *Psilophyton* because they bore spines. This choice agreed with the suggestions made by White but not with those of Halle. As will appear below, Lang became more attached to the use of *Dawsonites* as his work progressed. Lang examined axes of many sizes, from large, spiny ones to smooth, slender, repeatedly dichotomized ones bearing terminal sporangia. He was successful in studying small bits of carbon removed from sporangia. They revealed (Lang, 1931, pl. 28, fig. 24) a carbonized outer wall and an inner, thin, translucent layer which surrounded the spores. The inner layer reminded him of the persistent tapetum found in *Rhynia* and *Horneophyton.* Spores extracted from the sporangia ranged from 60 to 100 μ in diameter, were smooth, and were characterized by a darkened triangular area around the small trilete scar. In the same paper Lang described the detailed structure of the spines of *Psilophyton princeps* var. *ornatum* [now *Sawdonia ornata* (Dn.), Hueber, 1971], although he referred to them as *P. princeps.*

A year later Lang (1932, pp. 509-510) again reported sporangia with an outer wall and an inner, translucent layer. They came from Lower Devonian (Upper Siegenian) rocks in Scotland. The spores were somewhat larger, ranging from 75 to 100 μ in diameter. They were smooth or slightly papillate and showed some thickening around the trilete scar. Lang recognized that the fossils might be regarded as terminal parts of *Psilophyton* or as belonging to Halle's provisional genus *Dawsonites.* It is significant that this time Lang did not place them in *Psilophyton* as he had done the year before.

Lang's next contribution was made in collaboration with Croft (Croft and Lang, 1942). They described fertile axes from the Early Devonian (Siegenian) of Wales, some of which were smooth and some longitudinally striated. Both kinds bore lateral branches that subdivided several times and terminated in pendant sporangia. The fossils fitted Halle's diagnosis of *Dawsonites* and bore out the latter's prediction that numerous sporangia terminated the fertile branching system although Halle had not seen large numbers of sporangia. Croft and Lang's specimens (*e.g.* fig. 17, 18 on pl. 10) obviously provide a good illustration of Halle's concept of *D. arcuatus* (cf. Pl. 22, fig. 50). The authors also demonstrated that the wall of the sporangia consisted of an outer carbonaceous and an inner, translucent layer (cf. Pl. 23, fig. 52). This was the third time that such a sporangial wall had been associated with *Psilophyton* (or *Dawsonites*). Spores in these sporangia were in the smaller size range, 50 to 85 μ in diameter and were smooth. Croft and Lang in the same paper, described specimens bearing both spines and lateral sporangia under the epithet cf. *Psilophyton princeps.* Re-examination of these specimens by one of us (F.M.H.) has resulted in the conclusion that two or three different plants are included in the description and that certainly the fertile specimen in their figure 12 (BMNH V26507) is neither *Psilophyton princeps* nor *Sawdonia ornata* (Dn.), Hueber, 1971. The morphological characteristics of its sporangia and of its emergences related it more closely to *Crenaticaulis* Banks and Davis, 1969, than to the other genera. A new name is required for this fertile specimen.

Stockmans (1940) used Halle's provisional name *Dawsonites* in the restricted sense for monopodially and dichotomously branching axes that bore sporangia terminally, often pendant, on lateral branching systems. His specimens were collected at four Lower Devonian (probably Emsian) quarries and were clearly referable to *D. arcuatus.* Specimens from a fifth quarry he called *Dawsonites* sp. with the comment that they resembled *D. jabachensis* Kräusel and Weyland (1935) as well as *D. arcuatus.* In addition Stockmans provided good evidence that *Dawsonites* also occurs in early Middle Devonian strata. He illustrated (pl. 14, figs. 2-5) plants from two quarries and referred them to *Dawsonites* sp. but gave no further description because his monograph was concerned with Lower Devonian strata. We consider these to be good examples of *D. arcuatus.*

In 1930 (p. 75) Kräusel and Weyland used the name ?*Dawsonites* sp. for a narrow axis that bore two rows of (?) sporangia laterally. Dorf (1933, p. 246) suggested that this German material might be placed in *Bucheria* [now *Rebuchia* (Dorf), Hueber, 1970]. Both Halle (1936, p. 22) and Høeg (1942, p. 65) agreed with Dorf's suggestion. Kräusel and Weyland (1948, p. 91) agreed that *Dawsonites* was not intended to include spikelike fructifications. Earlier (1941, p. 54) they had remarked that their ?*Dawsonites* sp. might fall in the same group as *Barinophyton* or *Pectinophyton* and that it resembled *Zosterophyllum* as well. Certainly it is no *Dawsonites* and it has been relegated to doubtful species under *Rebuchia* (*Bucheria*) by Høeg (1967, p. 266).

In 1933 Kräusel and Weyland (p. 39) described another axis from the Middle Devonian Srbsko beds of Bohemia. It bore kidney- or club-shaped sporangia laterally along one side. They compared the specimen with *Taeniocrada, Zosterophyllum,* and *Hostimella racemosa* of Lang (1925) but rejected all three possibilities. Instead they chose to use Halle's provisional name *Dawsonites* in a wide sense to include almost any sporangia whose affinity is unclear. Thus they named their plant *Dawsonites bohemicus.* This use of the generic name marked a sharp divergence from the concepts of Halle and Lang. Obrhel (1961, p. 35) reexamined the type specimen of *D. bohemicus* and argued convincingly in favor of its reassignment to *Zosterophyllum* or *Gosslingia.* He chose the former name and made the recombination ?*Zosterophyllum bohemicum* (Kräusel and Weyland), Obrhel.

Kräusel and Weyland (1935, pp. 185-186) described a new species of *Dawsonites, D. jabachensis* from the upper Lower Devonian of Jabachtal near Lockmar in the Rhineland. In 1962 they described additional specimens from the Lower Devonian of Alken on the Moselle. They stressed the resemblance of its flat, ribbon-like branches, the arrangement of its sporangia, and its general organization to *Taeniocrada.* Yet they separated it from *Taeniocrada* because of the longitudinal striations on some branches and the structure of its sporangia. In our opinion it shares with *Dawsonites* only the terminal position of its sporangia. It differs sharply from *Dawsonites* in its lack of a lateral, dichotomizing fertile branch system. It also differs because its older branches are ribbon-like, its longitudinal striations are continued on to the sporangia, and its sporangia are single, not paired. We believe that a new generic name should be created for it.

In the same paper Kräusel and Weyland (1935, p. 186) assigned specimens from Lower Devonian (Siegenian) strata of Nellenköpfchen to *Dawsonites* sp. The plant consisted of a pseudomonopodially branching axis whose laterals forked only once. One lateral bore a single terminal sporangium. The inclusion of this material in *Dawsonites* also requires an unjustified broadening of Halle's concept. We suggest it be placed in another genus.

Høeg (1935) erected the species *Dawsonites ellenae* for sterile and fertile shoots from the Middle Devonian of Western Norway. Fertile shoots bore lateral clusters of rounded bodies (probably sporangia) that he interpreted as terminating the branches of several successive dichotomies. The sterile shoots bore laterals, recurved at the apex, rather comparable to those of *Aneurophyton.* Some spines were found on both sterile and fertile axes. Høeg was fully aware that he had to widen the limits of Halle's provisional genus but he preferred this to the erection of a new genus on limited material. We think, however, that a new generic category is indicated. One significant character separating *D. ellenae* from *Dawsonites* is its rounded sporangia.

Stockmans (1940) described a new species of *Dawsonites, D. minor.* Its lateral branches forked only one or two times before terminating in more or less spherical sporangia. As a result the sporangia appear to be grouped against the main axis. The shape of the sporangia and the paucity of divisions of its lateral branches distinguish it clearly from *Dawsonites* and, like *D. ellenae,* it would be better transferred to another genus.

Høeg (1942, pp. 31-32) compared some plants from the Upper (?) Devonian of Spitzbergen with Halle's *Dawsonites.* Their straight and longitudinally ridged axes bore repeatedly branched lateral axes some of which terminated in pendant sporangia. The shortness of the side branches; the fact that they fork immediately on leaving the main axis and that some of them terminate in flattened, leaflike tips while others terminate in "small clusters of simple, narrow sporangia" caused Høeg to suggest that his plants might represent a new genus related to Protopteridales. His plate 8, figures 4, 7, 8 includes the most *Dawsonites*-like of his illustrations. It is wiser, however, to exclude them from this genus, as he did, unless subsequent collections yield more convincing evidence.

Ananiev (1957) described briefly and illustrated Lower Devonian plants from southwestern Siberia under the tentative name cf. *Protopteridium minutum* Halle. Ananiev stated that his fossils represented the kind of plant Halle had called *Dawsonites arcuatus.* However, certain axes produced sterile laterals that terminated in at least two successive dichotomies. These laterals resembled the sterile "pinnules" of Halle's *P. minutum.* In his choice of name Ananiev was probably influenced more by the sterile branchlets than by the resemblance of the fertile parts to the *Dawsonites* of Halle and of Lang. Without seeing the original material we can only agree that it resembles *Dawsonites.*

Obrhel (1961) described a new species of *Psilophyton, P. kräuselii,* whose lateral branches forked in an open, dichotomous manner like those of Dawson's *P. princeps* of 1859. Axes of *P. kräuselii* were delicate, villous throughout, and terminated by large clusters of recurved, terminal sporangia. *P. kräuselii* (studied by H.P.B., in Prague, 1968) seems to combine some elements of Dawson's 1859 description of sterile axes of *P. princeps* with the major features of Halle's provisional genus for fertile axes, *Dawsonites.* It appears to be the first published specimen to display all of the critical characteristics of the external morphology of *Psilophyton.* But it must be emphasized that no histological details of any sort have been obtained from this species, no cuticle, no epidermis, no spores, no vascular tissue.

Just as Obrhel's *Psilophyton kräuselii* demonstrated a plant with the essential features of Dawson's original concept of *Psilophyton,* so did the work of Hueber demonstrate that *Psilophyton princeps* var. *ornatum* can no longer be retained in the genus. Hueber (1964b) reported lateral sporangia on *P. princeps* var. *ornatum* from Dawson's type locality and from deposits along the Abitibi River, near James Bay at the southern end of Hudson Bay, Ontario, Canada. In the same year Hueber (1964a) reported an exarch protostele (figured in Hueber and Banks, 1967) in this variety of *Psilophyton.* In 1971 Hueber erected the name *Sawdonia ornata* (Dn.) for specimens usually referred to P. *princeps* var. *ornatum.* Additional evidence of lateral sporangia on *Sawdonia* was provided by Ananiev and Stepanov (1968) who illustrated fertile specimens (labeled *P. princeps*) from Siberia.

Two major characters, exarch protostele and lateral sporangia with distal dehiscence, are shared by *Zosterophyllum* (Edwards, 1969), *Gosslingia* (Edwards, 1970a), and

*Crenaticaulis* (Banks and Davis, 1969). Banks (1968b) suggested that plants with this combination of characters be placed in a new subdivision, the Zosterophyllophytina. Thus the spiny axes described by Dawson in 1871 as *P. princeps* var. *ornatum* and shown by Hueber (1964a) to bear lateral sporangia differ sharply from Dawson's original diagnosis of *Psilophyton* as a plant bearing terminal sporangia. Their new name, *Sawdonia ornata* (Dn.), Hueber, 1971, and their classification in Zosterophyllophytina emphasize this distinction.

Returning to *P. princeps*, Hueber and Banks (1967) restudied available original material of Dawson at Redpath Museum of McGill University, Montreal. They selected a neotype for *P. princeps*. The specimen bears spines and lateral branch systems terminated by pairs of sporangia. It was illustrated by Dawson in 1871 as figure 103 on plate 9. We may recall that Halle (1916) and White (1905) had observed only scars of spines on fertile axes and not the spines themselves. This one observation led Halle to erect the new taxon *Dawsonites* and led White to the belief (now seen to be an error) that the terminal sporangia should be associated with the spiny axes called *P. princeps* var. *ornatum* by Dawson in 1871 (=*Sawdonia*). The spines of the two taxa are markedly different. Hueber (1968) showed those of *P. princeps* to be blunt-tipped and terminated by a cuplike depression. Lang (1931, pl. 27, figs. 3-12) showed the spines of *Sawdonia* (his *Psilophyton princeps* var. *ornatum*) to be glandular tipped. Hueber and Grierson (1961) found identical spines on *Sawdonia* (their *P. princeps*) in Upper Devonian rocks in New York. Hueber and Banks (1967) illustrated a terete, centrarch protostele for *Psilophyton*. *Psilophyton* with its centrarch xylem strand and lateral branch systems terminated by clusters of sporangia is sharply distinct from *Sawdonia* which has lateral sporangia and an exarch xylem strand. Banks (1968b) used these characters in distinguishing a new subdivision, Trimerophytina (for *Psilophyton* and *Trimerophyton*). It is completely different from Zosterophyllophytina.

Hueber (1968) demonstrated a membrane inside the sporangial cavity of *Psilophyton princeps*. Maceration released this membrane as a sac (cf. Pl. 23, figs. 53-55. The sac corresponds to the inner, translucent layer of sporangium that Lang demonstrated on three occasions (1931, 1932, and, with Croft, 1942). *Psilophyton princeps* can now be regarded as a clearly defined plant.

Andrews, Kasper, and Mencher (1968) recently described another species, *Psilophyton forbesii*, based on smooth main axes that bore spirally arranged lateral branch systems which forked equally or unequally. One fertile branch system was found near the sterile specimens. The authors assumed it belonged with the sterile axes and so illustrated it in their reconstruction. Unfortunately their material yielded neither histological nor anatomical details nor additional morphological data.

Banks (1968a) studied specimens collected at Röragen (Halle, 1916) that were identical to axes Halle had called *Hostimella*. Halle suspected that these axes were terminal parts of his *Psilophyton goldschmidtii* and Banks demonstrated the probable correctness of this view by finding a terete, centrarch xylem strand in some of them. Thus anatomy typical of *Psilophyton* has been found both in Norway and in Canada.

Ananiev and Stepanov (1968) reviewed the status of the generic name *Psilophyton* prior to receipt of the paper by Hueber and Banks (1967) which established a neotype specimen to validate the species *P. princeps*. Like White (1905) they urged the selection of Dawson's (1871) sterile axes, *Psilophyton princeps* var. *ornatum*, as the type of *P. princeps*. However, their specimens from Siberia were richly covered by lateral sporangia like those reported by Hueber (1964b) and by Croft and Lang (1942). White, on the contrary, assumed that the spiny axes bore terminal sporangia. Hueber and Banks showed that terminal sporangia were central to Dawson's concept of his genus. Thus according to International Rules of Botanical Nomenclature the selected neotype should bear terminal sporangia. We suggest, therefore, that the excellent specimens of Ananiev and Stepanov be transferred to *Sawdonia ornata* (Dn.), Hueber, 1971, and be placed in Zosterophyllophytina.

Numerous other species of *Psilophyton* have been named on the basis of sterile specimens. Some undoubtedly will be proven to belong to the genus and probably some belong to other genera. Our purpose has been to show that a) Dawson confused parts of two taxa representing two different subdivisions, b) Lang and Croft and Lang similarly had specimens of the two subdivisions almost inextricably confused, c) that it has taken over one hundred years to secure enough data to clarify the true situation, and d) that one must have more than dichotomizing, spiny axes to identify a specimen of *Psilophyton* or of *Sawdonia*. We do not propose here an exhaustive analysis of all plants previously assigned to the genus.

## LOCALITIES AND STRATIGRAPHY

Locality 1. Specimens in the Cornell University Paleobotanical Collection were obtained from various levels in the cliffs (Pl. 17, fig. 1) along the beach between Douglastown and Seal Cove (Anse aux Loups-Marins) on the south side of Gaspé Bay, Quebec, Canada. From the same general area we used an additional specimen in the paleobotanical collections of the United States National Museum that is recorded as USNM loc. 14251, a site 48°40′32″ North and 64°20′8″ West, Range I Bois Brulé, Douglas Township, Gaspé, Quebec, Canada. McGerrigle (1950) included a useful map of the area: Malbaie Sheet No. 665.

The fossiliferous horizons belong to the continental Battery Point Formation which is generally regarded as Emsian to early Eifelian in age (McGregor, 1967, 1973). The lower (older) assemblage is similar to Lower Devonian assemblages at other localities in the world. In the middle of the Battery Point Formation, with no evidence of a stratigraphic break, the lower assemblage is replaced rapidly by one containing species characteristic of Eifelian and Givetian strata in Scotland and the U.S.S.R. Similar rapid floristic changes during Emsian have been recorded at other localities (see McGregor, 1967, p. 179). It is not yet clear whether the upper part of the Battery Point should be regarded as early Middle Devonian (Table 1). Our fossils are associated with the lowermost part of McGregor's (1967) upper spore assemblage (McGregor, Geological Survey of Canada Report No. F1-7-1972-DCM pers. comm.) and, therefore, are probably from Lower Devonian, late Emsian strata. Nevertheless we must emphasize that their position is close to the Lower-Middle (Emsian-Eifelian) Devonian boundary because there is no proof that the abrupt change in composition of the spore flora coincides with the Lower-Middle Devonian boundary. McGregor (1967) suggested the interesting possibility that a new flora rather suddenly began to invade and displace the earlier flora. This floristic change could have occurred late in Early Devonian time or early in Middle Devonian time. It need not have occurred simultaneously with an Early-Middle Devonian boundary. The fossil plant remains occur in cobbles and boulders of clay that were laid down in coarse, water-deposited sands and pebble conglomerates. The sediments were subsequently consolidated then lithified by precipitation of calcium carbonate. It would appear, at the locality, that mineralization and resultant petrifaction of the plant remains took place after deposition of the cobbles and boulders and not prior to their removal from an earlier site of burial. The specimens in the USNM collection differ only in that the sediments enclosing the plant remains are a medium-grained sandstone rather than mudstone.

Locality 2. This locality has been assigned number 6435 in the records of the Department of Energy, Mines, and Resources of the Geological Survey of Canada in Ottawa. It is near latitude 50°13′ North and longitude 81°38′ West on the Abitibi River, Moose River Basin, James Bay Lowland, Ontario, Canada. Precisely, the site is an eight to twelve inch stratum of micaceous, medium-to fine-grained sandstone on the west bank of the River, below Sextant Rapids, above Coral Rapids, and directly opposite the south end of a red outcrop, 400 feet in length, located on the eastern bank. Maps as references in locating the site are entitled "Southern Part of James Bay Lowland - Index Map of Fossil Collections" and Map No. 1952-1953 - Southern Part of James Bay Lowland" (geologic map) and are attached to Martison's report (1953) on the geology and petroleum potential of the area. This horizon is a part of the non-marine Sextant Formation which is considered to be middle to late Emsian age (McGregor, Sanford, and Norris, 1970) (Table 1) on the basis of dispersed spores.

The first identification of plant fossils from the Sextant Formation is found in Martison's report (1953, p. 30) where the late W. A. Bell is cited as identifying *Drepanophycus spinaeformis* Goeppert and sympodially branched, longitudinally striated stems probably conspecific with *Dawsonites arcuatus* Halle. The latter specimens were probably examples of our new *Psilophyton dawsonii.* Plant remains were found to be locally abundant at several horizons along the outcrops on the west bank of the river during field studies undertaken by McGregor and Hueber in 1961. Hueber (1964b) added *Sawdonia ornata* (his *Psilophyton princeps* of 1964b) to the floral list.

## MATERIALS AND METHODS

In the early 1930's the late Professor L. C. Petry of Cornell University discovered calcareous cobbles embedded in the sandstone cliffs at Locality 1 (Pl. 17, fig. 1). His collecting, several trips by Banks to the same locality, and more widely ranging expeditions by Hueber in New Brunswick and Ontario have resulted in a good collection of *Psilophyton.* The present account is confined to two localities in order to keep its size manageable. Running more or less parallel through the limey clay cobbles and boulders are petrified parts of *Psilophyton.* Selected specimens were cut into blocks, numbered, and peeled serially using standard coal ball techniques. Where measurements were essential, as with sporangia, the blocks were ground on a Croft parallel grinder. Altogether several thousand peels have been made and examined.

Some axes were macerated out of the matrix using hydrofluoric acid which, because it does not dissolve the carbonates in the lumens of the cells, left small branches intact,

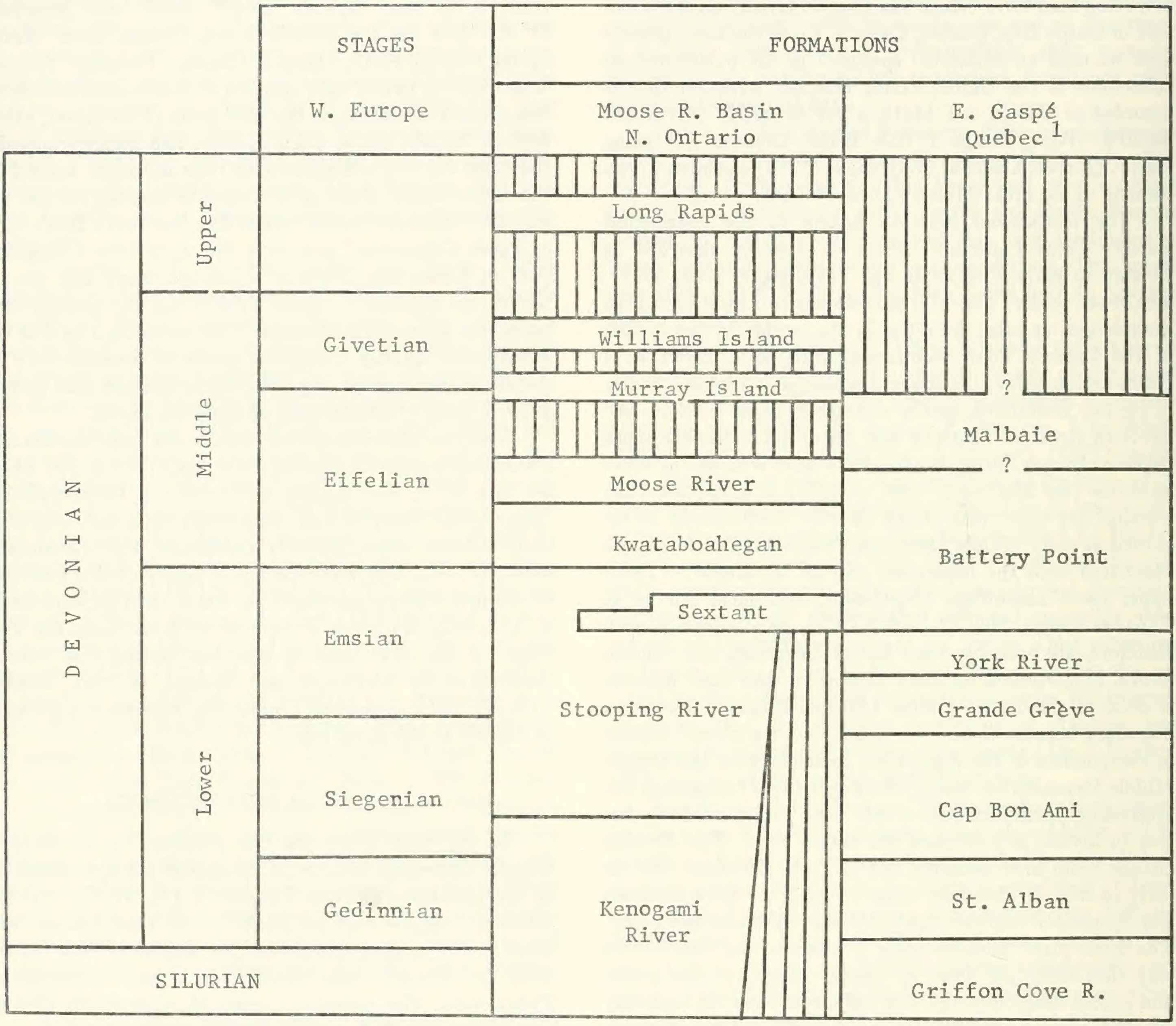

Table 1. Correlation chart showing the position of the Sextant Fm. at Abitibi River and the lower portion of the Battery Point Fm. on the Gaspé Peninsula. From McGregor, Sanford, and Norris (1970). [1]Modified from Boucot, *et al.*, (1969).

although often coated with insoluble whitish fluorides. These branches were then imbedded in bioplastic, a methyl methacrylate resin, as visual evidence that successive dichotomies were produced at right angles to one another (Pl. 17, fig. 5).

Other fragments were prepared by bulk maceration in concentrated hydrofluoric acid, washing, and clearing in Schulze's solution ($HNO_3$ and $KClO_3$). Clearing was also carried out using hydrogen peroxide or dilute sodium hypochlorite (Pl. 23, figs. 53-55).

Both axes and sporangia were demineralized, embedded in paraffin and microtomed (Pl. 18, fig. 16, Pl. 19, fig. 24, Pl. 23, fig. 52).

Plants at the Abitibi River locality occurred as compressions in medium-to fine-grained sandstone with occasional lengths of axis preserved by iron pyrite. Some were uncovered (Pl. 17, fig. 3) using steel needles under a binocular dissecting microscope at 10-30X magnification (dégagement of Leclercq, 1960). Petrified axes were embedded in plastic, sectioned, impregnated with resin, and ground. Grinding was carried to the level of 800 grit and the surfaces then polished with chromium oxide on a glass plate.

Sporangia were macerated from the matrix using concentrated (48%) hydrofluoric acid. After several washings through ten changes of water, some of the sporangia were stored in glycerine jelly and others were treated with Schulze's solution. Oxidation in Schulze's solution disintegrated the sporangium walls and freed the spore masses or, in the case of empty sporangia, freed the saclike membrane that surrounded the spore masses. Specimens were mounted as temporary mounts in glycerine jelly for the purpose of photography.

Photography was done on a Zeiss photomicroscope and a Leitz Aristophot.

## DESCRIPTION

### A. ANATOMY

1. Histology

Main axes are frequent in the Gaspé cobbles. In transverse section they are slightly compressed because the inner cortex has usually been lost by decay (Pl. 20, fig. 30). When living, the axes were certainly terete. A single, cylindrical strand of primary xylem and an outer, resistant cortex are always preserved (Pl. 20, figs. 30, 31), a narrow zone of phloem and a parenchymatous inner cortex occasionally (Pl. 18, fig. 18, Pl. 19, fig. 19).

The xylem strand when not branching consists of a single, central protoxylem surrounded by metaxylem (Pl. 20, fig. 30). Maturation is centrarch. Protoxylem consists chiefly of narrow spiral and scalariform elements (Pl. 19, figs. 21, 22, 25). Metaxylem tracheids are long, tapering, and approximately 60-80$\mu$ in diameter. All walls are scalariform (Pl. 19, figs. 23-26). Sectional views (Pl. 19, figs. 27-28) demonstrate that the scalariform bars are bordered, hence that the tracheids have scalariform bordered pits. Between the scalariform bars the deposition of additional secondary wall material has outlined horizontal rows of circular, pitlike areas (Pl. 19, figs. 23-24). This additional wall material may even resemble vertical striations (the Williamson's striations of lepidodendrids) between the scalariform bars (Pl. 19, fig. 25) although this is not a frequent appearance. One or two rows (Pl. 19, figs. 23-24, 26) of pitlike areas are frequent, three rows are seen rarely. The number of pitlike areas in a row varies from 10-14; usually the wider the tracheid, the more numerous the circular areas.

Phloem is only rarely preserved immediately centrifugal to the xylem. It is a uniform zone composed of two to six layers of thin-walled, narrow, tangentially elongated cells (Pl. 19, fig. 19). In longitudinal section they are vertically elongated, with slightly oblique end walls (Pl. 19, fig 20). No sieve areas have been observed.

Inner cortex is best preserved in slender branchlets where it consists of narrow, thin-walled, loosely arranged parenchyma cells that are rounded or polygonal in transverse section and vertically elongate-rectangular in longitudinal section (Pl. 18, fig. 18).

The absence of inner cortex often results in a change of position of the xylem strand during fossilization. It may appear in an eccentric position (Pl. 20, fig. 34). Simultaneous twisting of the strand sometimes results in apparent changes in the orientation of the protoxylem strands and consequently of the emission of lateral branches.

The outer cortex is usually well preserved (Pl. 18, figs. 12-14). It is composed of large, thick-walled cells which in longitudinal section have transverse to slightly oblique end walls (Pl. 18, figs. 16, 17). It is thus collenchymatous in appearance. In some areas this thick-walled tissue is partially replaced by parenchyma (Pl. 18, fig. 12). Occasionally in such areas the cells appear to have disintegrated (Pl. 18, fig. 15). Often these areas are completely empty of cells or of cellular debris (Pl. 18, fig. 13). If we recognize various appearances of the cortex internal to the stomata as developmental stages (as in Pl. 18, figs. 12, 13, 15) it seems clear that substomatal chambers arise ontogenetically under the stomata whose guard cells can sometimes be recognized (Pl. 18, fig. 13).

Epidermis is rarely recognizable. In transverse section the cells are small and rectangular (Pl. 18, fig 14). In longitudinal section they are longer than broad (Pl. 18, fig. 11).

The hypodermal nature of most of the outer cortex and the substomatal chambers suggest that the inner cortex functioned as assimilating tissue.

2. Dichotomy of the main axis.

Below a branching the xylem strand is terete and has a single, central protoxylem. In successively higher sections the protoxylem is divided equally, the two resulting strands are gradually further apart, the entire primary xylem is constricted, and finally there are two main strands each with its single, central protoxylem (Pl. 20, fig. 29). At a still higher level the axis itself is constricted and then separated into two equal branches.

3. Anatomy of fertile lateral branch systems.

The first indication that a main axis will produce a fertile lateral branch is a tangential increase in its protoxylem. Soon one strand of protoxylem is free in the primary xylem strand (Pl. 20, fig. 31). In successive sections this lateral protoxylem is further from the original strand (Pl. 20, fig. 32) and finally is free in its own metaxylem (Pl. 20, fig. 33). The protoxylem of the main axis remains elongated tangentially (Pl. 20, fig. 32) thus demonstrating that the next higher fertile branch will be produced on the opposite side of the axis, a distichous arrangement. The lateral structure is now a circular branch trace with one central protoxylem. Higher up the branch trace is rectangular in shape and its protoxylem has become elongated (Pl. 20, fig. 34). By the time the branch is free from the main axis its protoxylem strand has dichotomized twice (Pl. 20, fig. 35) and soon there are three separate xylem strands (Pl. 20, figs. 36, 37). These two dichotomies are expected to result in three branches and at first this seems possible (Pl. 21, fig. 38). However, at a higher level, one of the three branches usually aborts. In this case it is the central branch that is aborting (Pl. 21, fig 39). Each of the two branches that remains again undergoes two close dichotomies and again one of the three resulting branches aborts (Pl. 21, fig. 40). The fertile branch system now consists of four equal branches. On a compression specimen that branches in this way one sees what appear to be two, successive dichotomous forkings often with a peculiar fragment of a branch between the arms of the dichotomies. (Pl. 17, fig. 4). We refer to these unusual branchings as *double dichotomies* in order to emphasize that two dichotomies do occur each time and to explain the appearance of an aborted branch between two fully grown branches. We have observed these double dichotomies so many times that we believe they represent the usual pattern for the first two divisions of the fertile branch system of *Psilophyton dawsonii*. It seems likely that in exceptional cases there is no abortion and three branches develop from the double dichotomy.

Higher on the fertile branch system all forkings are strictly single dichotomies at successively closer intervals until all branches are terminated by sporangia. The beginning of one such dichotomy is shown in figure 41, Plate 21. Transverse and longitudinal sections of the final dichotomy whose tips bear sporangia are shown in figures 42, 43, Plate 22. It is clear (Pl. 22, fig. 43) that a large vascular strand extends into the base of each sporangium. Counting each double dichotomy as one branching this last forking (Pl. 22, figs. 42, 43) is the sixth and six seems to be the usual number of successive branchings of the fertile branch system.

Several features of the lateral branching system must be emphasized. 1) The branch trace is always rectangular in outline while its surrounding cortex is still attached to the main axis. This enables us to recognize the base of a fertile system even when its distal branchlets and sporangia are not preserved. 2) The first two divisions of the fertile system are closely spaced "double dichotomies" usually characterized by the abortion of one of the three resulting branches. 3) Successive divisions (six in all) of the fertile system occur at right angles, producing a three-dimensional branch system.

4. Anatomy of vegetative lateral branches.

One specimen has provided an unusually well-preserved example of extensive vegetative branching (Text-fig. 4). A large axis dichotomizes near the base of the specimen and the two new axes continue without change in diameter to the apex of the cobble. Both new axes produce lateral vegetative branches, one of them (B) giving rise to seven branches in the short vertical distance of 13-15 mm. This burst of branching is described in Part 3b - branch B and illustrated by Text-figures 9-12. Its good preservation permits a brief discussion of anatomical changes associated with the vegetative branching.

The stele of branch B below the level of profuse branching has a single, small protoxylem strand. Higher up it is enlarged and then much enlarged (Text-figs. 9d-g; Pl. 24, figs. 65, 64, 68). Two zones of primary xylem are clearly evident, a large, peripheral mass of metaxylem tracheids and an inner group of smaller protoxylem elements (Pl. 24, figs. 64, 68). The outline of the protoxylem soon becomes irregular and its continuity is broken during the rapid development of branch traces (Text-figs. 9f, g; 10a-c; Pl. 24, figs. 64, 63).

Traces to the sterile branches are essentially like the xylem of the main axis, circular in outline and with centrarch maturation (Text-figs. 10a-e; Pl. 24, fig. 62). Some of them are followed in a long series of peels, some disappear after a few peels, and one (No. 7 in Text-figs. 10b-e) fades out before it reaches the outer cortex of the parent axis. The bundles follow a steep course outward and as a result several are included within the cortex of the main stem (Text-figs. 10b-d).

The chief interest in this type of branching is the striking modification of the terete, centrarch xylem strand. The usual modification is a tangential elongation of the protoxylem (Pl. 20, fig. 31) which is related to the production of branches alternately first on one side then on the other, a distichous arrangement, basically a spiral referable to a ½ phyllotaxy. The modification found in the area of vegetative branching is a considerable increase in the size of the protoxylem and its angularity in transverse section (Pl. 24, fig. 64). This change in contour of protoxylem is associated with the production of a large number of lateral branches in a close spiral and within an extremely short vertical distance. The enlarged central mass of xylem (Pl. 24, fig. 65) is associated with the origin of traces to this large number of lateral branches and by the time all of them are free, the individual traces are much reduced in size (Pl. 24, fig. 62) although clearly different from the usual pattern found in the axis (Pl. 24, fig. 69). Only one strand issuing from this large central mass assumes the typical configuration for an axis in the area of fertile branching. That is the one that continues the main axis (B) above the region of vegetative branching. It is shown in Plate 24, figure 66 which can be compared with Plate 24, figure 69 and Plate 20, figures 30-32. Plate 24, figure 66 represents a level slightly higher on the plant than Plate 24, figure 62. Thus *Psilophyton dawsonii* branches in a tight spiral and a loose spiral (alternate, distichous arrangement) depending on the level at which it is studied.

Also noteworthy is the rapid decrease in diameter of branch traces in the area of vegetative branching. Many of them arise as fairly large bundles but diminish rapidly in size in the cortex. See for example trace to branch 6 on Text-figure 10c, d and e or trace to branch 7 on the same figures. The latter disappears altogether in the cortex leaving no external evidence of its presence.

A further modification of the terete centrarch xylem strand is the apparent radial alignment of some of the increased metaxylem. This is shown well in Plate 24, figure 63 on axis B and near the origin of traces 5 and 6. This simulation of secondary xylem is perhaps only associated with the large increase in extent of the xylem strand. Nevertheless it is a tendency worthy of note. Plate 24, figures 64, 65, 66, 69, are all made at the same magnification in order to demonstrate the extreme enlargement of the central xylem just below the level of rapid vegetative branching and to contrast this large size with the usual size in the region of fertile branching (Pl. 24, fig. 69).

Plate 24, figure 66 shows a terete xylem strand above the vegetative branching, with an elongated protoxylem strand and a free branch trace (left). Slightly higher the branch trace is contained in its own cortex, is rectangular, and has three protoxylem strands (Pl. 24, fig. 67). This is the first double dichotomy at the base of a fertile branch.

## B. MORPHOLOGY

### 1. Fertile lateral branch systems; based on Douglastown, Gaspé specimens: holotype 190, paratype 191.

#### a. Gross

Our reconstruction (Text-fig. 13) shows a much-branched plant whose fertile lateral branches are produced alternately and distichously along the main axes. On the basis of serial peels we have reconstructed fertile lateral branches as three-dimensional systems with, usually, six successive divisions, hence seven orders of branch, the last of which are the short stalks of each sporangium. The first two divisions externally may resemble single dichotomies but as described earlier each one is in fact two closely spaced dichotomies of which only two branches develop. Sometimes the aborted remnant of the third branch can be seen between the two developed branches (Text-fig. 3x). Subsequent divisions are successively closer together and are dichotomous or slightly unequal. From the peels we conclude that these divisions occur at 90° angles to one another, resulting in a three-dimensional system. In order to confirm this we macerated some specimens in HF-HC1 and extracted vegetative apices that retained two to four dichotomies. These were embedded in bioplastic (a methyl methacrylate resin) and photographed (Pl. 17, figs. 5, 6). All axes examined demonstrate that the plane of the dichotomies did in fact rotate 90° at each division.

There is of course much variation in the distance between successive dichotomies but Table 2 gives an approximation of the size of branching system.

#### b. Internal[1]

Anatomically the production of a fertile lateral branch is indicated for the first time by a tangential enlargement of the protoxylem (Text-fig. 3c; 3x; Pl. 20, fig. 31). Slightly higher the new protoxylem is surrounded by its own metaxylem and a bulge appears on one side of the xylem strand (Text-fig. 3d; Pl. 20, fig. 32). Still higher a circular strand with a central protoxylem is free from the parent strand (Text-fig. 3e; Pl. 20, fig. 33). Slightly higher the new strand is located in its own axis. (Text-fig 3f; Pl. 20, fig. 34) and it is rectangular in shape. The rectangular shape is partly the result of a tangential elongation of its protoxylem. The

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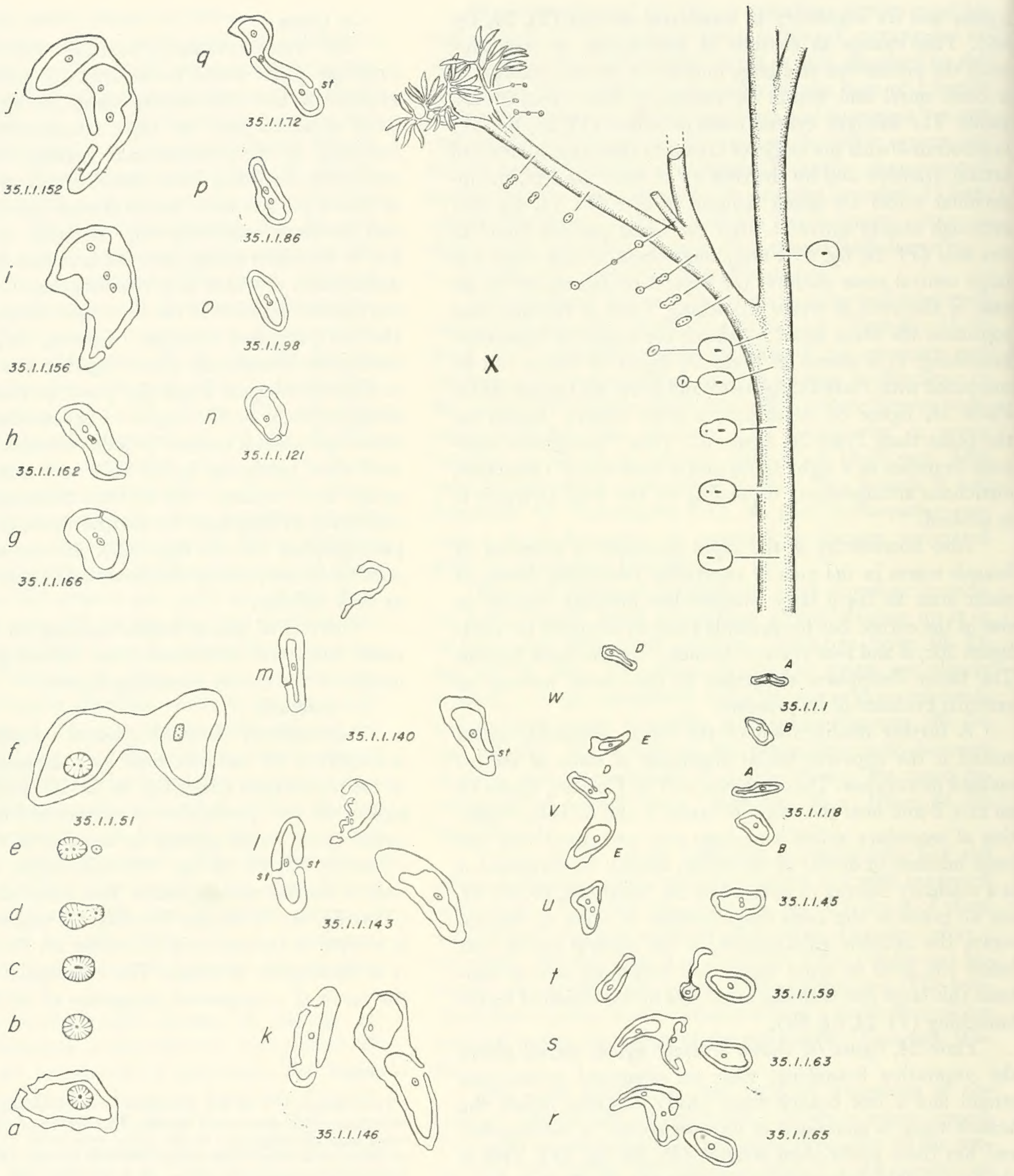
[1] Text-figures 3, 5-12 are provided in order to supplement the reconstructions with anatomical details. Text-figures 5-12 are drawn to the same scale. Photographs of the peels were made at an enlargement of 20 times. Drawings were made from the photographs. These were reduced photographically. Thus all axes illustrated are shown in the same relationship to one another that they had in the peels and in the cobble except Text-figure 12 which is explained in the text and legend. Only the vascular strands and outer cortex are represented. Protoxylem is shown by a point or, if its size is greater, by an elongated solid line. Occasionally the number of protoxylem cells is much increased. This is shown by cross hatching and the surrounding metaxylem is then indicated by radial lines (see Text-figure 9).



Text-figure 3. Diagrams drawn from peels at successively higher levels from main axis to origin of fertile branches to sporangia. a) main axis; b-e) origin of trace to fertile branch, xylem only; f) with cortex; g-m) two dichotomies of trace followed by abortion of central branch; n-t) similar "double dichotomy" of one of the two healthy branches in m — the other healthy branch divides similarly; u-w) first dichotomy of the two healthy branches in u (subsequent dichotomies omitted); x) reconstruction based on a-w.

Table 2. Length of successive axes of the fertile branch system and of sporangia.

| structure | length (mm) |
|---|---|
| sporangia | 3.0-4.2 |
| axis 7 (in stalk of sporangium) | 0.5-0.75 |
| axis 6 | 1.5-2.0 |
| axis 5 | 1.5-3.0 |
| axis 4 | 3-5 |
| axis 3 | 5-20 |
| axis 2 | 5-20 |
| axis 1 (up to the first double dichotomy) | up to 30 |

surrounding metaxylem is limited to two or three layers of cells. It must be emphasized that we have found this rectangular bundle repeatedly in sections at the base of fertile lateral branch systems. It is so constant that we are able to use it as an indicator of fertile branches even when the distal part of the fertile system was not preserved in a specimen. The rectangular bundle has a narrow, tangentially elongated area of protoxylem which divides into three separate strands. At higher levels first one and then the other lateral protoxylem group becomes a new bundle (Text-fig. 3 g-i; Pl. 20, figs. 35-37). Each of the three tiny new bundles is terete and centrarch. While still in a common cortex the distance between the two dichotomies is reflected by the distance between the three bundles. Shortly one, and then the other, of two axes becomes free (Text-fig 3k, 1; Pl. 21, fig. 38). We refer to this pair of close branchings as a double dichotomy. At this point it is especially interesting to note that usually one of the three resulting branches diminishes in size and aborts. This phenomenon is illustrated in Text-figure 3 l and m; Plate 21, figures 39, 40. The aborted branch has been followed in one case for more than 5 mm but it is usually shorter. This may account for the failure to observe it on most compression specimens of *Psilophyton*.

We follow now the subsequent branching of *one* of the two remaining branches starting in Text-figure 3n. This branch, as well as the other which is not illustrated, divides in exactly the same fashion as before. The process of successive, close dichotomies (Text-fig. 3n-t; Pl. 21, fig. 40) followed by the abortion of one of the three resulting axes is repeated. The fertile system now consists of four slender axes (two of the four are shown in Text-figure 3x and one of the four in Pl. 21, fig. 41).

From this level upward four successive dichotomies occur singly. The first of these subsequent dichotomies is illustrated in Text-figure 3u-w. At the level of 3w, there is a total of 8 small branches. The next dichotomy results in 16 smaller branches and we find usually a third forking which results in a total of 32 still smaller branches. Each of the 32 dichotomizes into a pair of terminal sporangia. (Pl. 22, figs. 42, 43). Counting the first two closely spaced "double dichotomies" each as one, this means the fertile system often shows 6 successive forkings and bears 64 sporangia, arranged in 32 pairs. The number 64 can vary by any one of several minor changes. One dichotomy may be suppressed, a dichotomy may be added somewhere in the system, or one or more sporangia may abort. Finally, the number of sporangia would be increased markedly if the third branch at either of the first two double dichotomies were to develop rather than aborting. We have not actually observed these larger numbers but some specimens seem not to show abortion of a branch during the lower divisions and lead us to expect that the increased numbers may actually occur from time to time.

The histology of the smaller branches is similar to that described for the larger axis. Their xylem strands are still terete and centrarch. Their inner cortex is usually not preserved. When preserved it consists of narrow, thin-walled cells. Their outer cortex is reduced to two or three layers of hypodermal tissue and stomates and epidermis are often seen clearly.

The fusiform sporangia are borne in pairs on short stalks. They range from 3 to 5 mm in length and 1.0-1.5 mm in width. They widen from a narrow base and then taper distally (Pl. 22, figs. 43, 50, Pl. 23, fig. 51), sometimes to a point as though they were terminated by a spinelike beak which usually broke off during fossilization.

The distance between successive dichotomies of the fertile branching system is progressively less distally. Hence young sporangia often appear in close clusters (Pl. 22, fig. 44). As maturation continues the pairs of the clusters become somewhat more distant (Pl. 22, fig. 49). This ontogenetic change is reflected in the attitude and content of sporangia as well. Sporangia can be found on the broken surface of specimens from Douglastown, Gaspé (Pl. 22, fig. 50). These recurved, but not tightly recurved sporangia, still contain spores and represent the often figured attitude of sporangia of the genus. On Text-figure 13 however some fertile branching systems are shown terminated by sporangia in various attitudes, recurved, horizontal, and erect. This reconstruction is a faithful representation of empty sporangia that were revealed only in serial peels. The fact that all have dehisced and that they are no longer in tightly recurved groups leads to the conclusion that as sporangia matured and dehisced, they were borne in a more widely spread cluster. Specimens from Abitibi River to be described below confirm this conclusion.

Most striking is the resemblance of the anatomical structure of sporangia to that of vegetative axes as shown by transverse and longitudinal sections just distal to, or at, the final dichotomy of the xylem at the base of the sporangia (Pl. 22, figs. 42, 43). One branch of xylem enters each sporangium. Clearly the ratio of diameter of xylem to diameter of axis is the same in the base of the sporangia as in large axes, and this xylem extends up to the sporogenous tissue of the sporangium. Similarly the sporangial wall itself (Pl. 22, figs. 44-48) is comparable to the cortex of the axes. The outer two or three layers of cells are hypodermal like the corresponding layers in the axis. The inner two to four layers are parenchymatous (Pl. 22, figs. 44-47) like the inner cortex of axes. Even stomata and substomatal chambers are like those of axes (Pl. 22, fig. 45). Epidermis is rarely observed but a cuticle-like layer is sometimes present.

Maturation of sporangia involves breakdown of parenchymatous wall layers (Pl. 22, figs. 44-48). Simultaneously the inner tangential walls of the innermost parenchyma break away as an intact membrane (Pl. 22, fig. 48). This membrane normally remains inside the sporangium, attached at either side of the region of dehiscence (Pl. 22, fig. 49), and often breaking opposite the region of attachment. Plate 22, figure 49 shows a cluster of four dehisced sporangia more distantly arranged than the four immature ones shown in figure 44, Plate 22. The mature sporangia illustrate the dehiscence that is longitudinal along facing surfaces. This results in pairs of C-shaped, empty sporangia (Pl. 22, fig. 49).

Intact sporangia are found on compression specimens collected at the Abitibi River locality (Pl. 23, fig. 51). Some of these sporangia were demineralized, embedded in paraffin, and sectioned on a microtome. The sections revealed the same inner, translucent layer that Lang found in the sporangia from three different localities inside a thick carbonized wall (Pl. 23, fig. 52). In order to relate these two layers to the structure seen in petrifactions, similar sporangia were macerated and thin sacs filled with spores were released from them. Full sacs are shown on figure 51, Plate 23, and at a higher magnification in figure 53, Plate 23, where both full and empty sacs are illustrated. Both were obtained from sporangia by maceration. Sporangia from Douglastown were macerated in the same way in order to compare plants from the two localities. Again we obtained both intact membranes containing spores and membranes that were free of spores (Pl. 23, figs. 54, 55). We believe that the cellular pattern on the membranes is that of the inner, parenchymatous wall cells of the sporangia. The anticlinal walls of these parenchyma cells broke down but their inner tangential walls remained connected to form the sac. The sac may have been reinforced by deposition of end products of the disintegration of the tapetum.

Masses of spores, apparently representing all those found in one sporangium, are often abundant in the matrix (Pl. 23, fig. 57). It is not possible to determine whether they were released naturally by dehiscence or whether they were masses of immature spores freed by the decay of sporangial walls. The abundance of these spore masses is predictable when it is recognized that the sporangia are borne in masses of up to 64 or more, the number dependent on normal or abnormal branching of the lateral axis.

Spores occur variously in our material, some *in situ* in attached sporangia, some in masses that were released naturally from sporangia, and some removed from sporangia by maceration. Many of them, both inside and out of sporangia, have been compressed in a polar direction, resulting in a cup-shaped object with the firm proximal surface pressed against the distal surface. This compression can occur while spores are still arranged in a tetrad. As a result, the trilete mark appears to be on the distal surface (Pl. 23, fig. 60), where it is seen through the transparent distal exine.

The spores range from 40-75 $\mu$ in diameter. The equatorial contour (amb) is circular to subcircular (Pl. 23, figs. 58, 56). Contact areas are distinct, outlined by a simple trilete mark which extends ½ or more the length of the radius. Its connection to the curvaturae is not obvious. Curvaturae usually follow the equatorial margin. The trilete mark is composed of three simple commissures, surrounded, or outlined, by a darkened triangular area (Pl. 23, figs. 58, 56, 59, 61), whose sides are variously straight or concave. The commissure is occasionally split open (Pl. 23, fig. 61).

The exine of the spores is smooth and unornamented. This statement requires some explanation. Within the sporangium, while the spores are still in tetrads some form of deposit is laid down on and around the spores (Pl. 23, figs. 59, 60 at C). This envelope appears to be minutely ornamented. However, it is not dispersed with the spores. Occasionally, for example, the envelope may break away from the spore as a thimble-shaped structure. This is illustrated (Pl. 23, fig. 58) in the case of a spore that has separated from a tetrad. Besides the spore, which now has a smooth exine, lies part of the envelope that formerly covered it. The envelope or thin membrane may be a perispore which is just as prominent between the spores (Pl. 23, fig. 59) as it is on them (Pl. 23, fig. 60 at C). It may be a product of tapetal fluids. In any case, the exine of the spores, once freed from the surrounding membrane, is smooth (Pl. 23, figs. 56, 58) and the spores fit the Infraturma Laevigati. These spores if found as sporae dispersae would be placed in *Retusotriletes* (Naumova), emend Streel, 1967, and they are probably closest to *R. triangulatus* (Streel), 1967. Following Mortimer (1967) they would more likely be placed in *Phyllothecotriletes*.

Both Streel and Richardson examined the spores in our material and Streel published (1967) the illustration we use as figure 60, Plate 23, as well as one essentially identical to our figure 58, Plate 23. Richardson (1969) figured a *Retusotriletes triangulatus* from the Welsh Borderland on his plate 11-2 as figure 1 and commented (p. 211) on its resemblance to our spore without its perispore. When the perispore is still present he considered that our spores resemble *?Perotriletes* which is illustrated on his plate 11-3, figure 7. This figure can be compared with our figures 59, 61, Plate 23. Richardson and Lister (1969, pp. 217-218) also commented on the resemblance of our spores to *Cyclogranisporites* sp. from the lower Battery Point Formation, Gaspé Peninsula, as illustrated by McGregor and Owens (1966, pl. 2, figs. 18, 19). Those figures compare favorably with our fig. 61, Plate 23. *Retusotriletes* sp., (McGregor and Owens, 1966, plate III, fig. 1) is the smooth type (perispore removed) that ours resembles most closely. Thus despite the vagaries of identification of spores, it seems that we can be relatively confident of our interpretation and identification.

## 2. Fertile lateral branch systems — Abitibi River

Our reconstruction of fertile branches of *Psilophyton dawsonii*, made from several thousand peels, receives striking confirmation from the discovery of identical branching systems preserved as compressions, partially pyritized, along the Abitibi River, northern Ontario, Canada. The fossils occur in a soft sandstone ideally suited to the uncovering technique of Leclercq (1960). Hueber demonstrated the production of fertile branch systems in an alternate, distichous arrangement along a main axis (Pl. 17, figs. 2, 3). On the proximal divisions of the fertile branch he found evidence of abortion thus indicating "double dichotomies" as on the Gaspé Peninsula. This feature is illustrated specifically by the abortion we found in Halle's Röragen material (Pl. 17, fig. 4). Subsequent divisions of the Abitibi branches were single dichotomies and they occurred at a 90° angle to one another producing a three-dimensional system. This meant that as branchlets were uncovered, it was necessary to remove certain of them in order to uncover more deeply in the matrix. Where possible the sporangia that were removed were treated with HF and preserved in glycerine jelly. Figure 3, Plate 17, therefore, shows the end result, many branchlets and sporangia having been removed and counted before reaching the stage illustrated. Ultimate branchlets were terminated by pairs of recurved sporangia (Pl. 23, fig. 51) like those found on the Gaspé specimens (Pl. 22, fig. 50).

The anatomy of the Abitibi material is also identical to that from Gaspé. A portion of a series of sections preserved by pyrite is shown in Plate 17, figs. 8-10. Protoxylem, metaxylem, and branch trace all act exactly as in our Gaspé peels. Metaxylem tracheids (Pl. 17, fig. 7) show the same scalariform pitting and interconnections between the bars producing pitlike areas. The branch traces followed outward undergo two close dichotomies like those shown in figures 36-40, Plates 20-21, for Gaspé material.

Details of sporangia revealed by maceration and by microtome sections of paraffin embedded sporangia further confirm the identity of the two collections. Inside each sporangium is a thin membrane (Pl. 23, fig. 52) that can be released by maceration. The membrane proves to be a sac either full or empty of spores (Pl. 23, fig. 53). Our Gaspé peels shows the same membrane (Pl. 22, figs. 48-49) and our macerations disclose the same kind of sac (Pl. 23, figs. 54, 55).

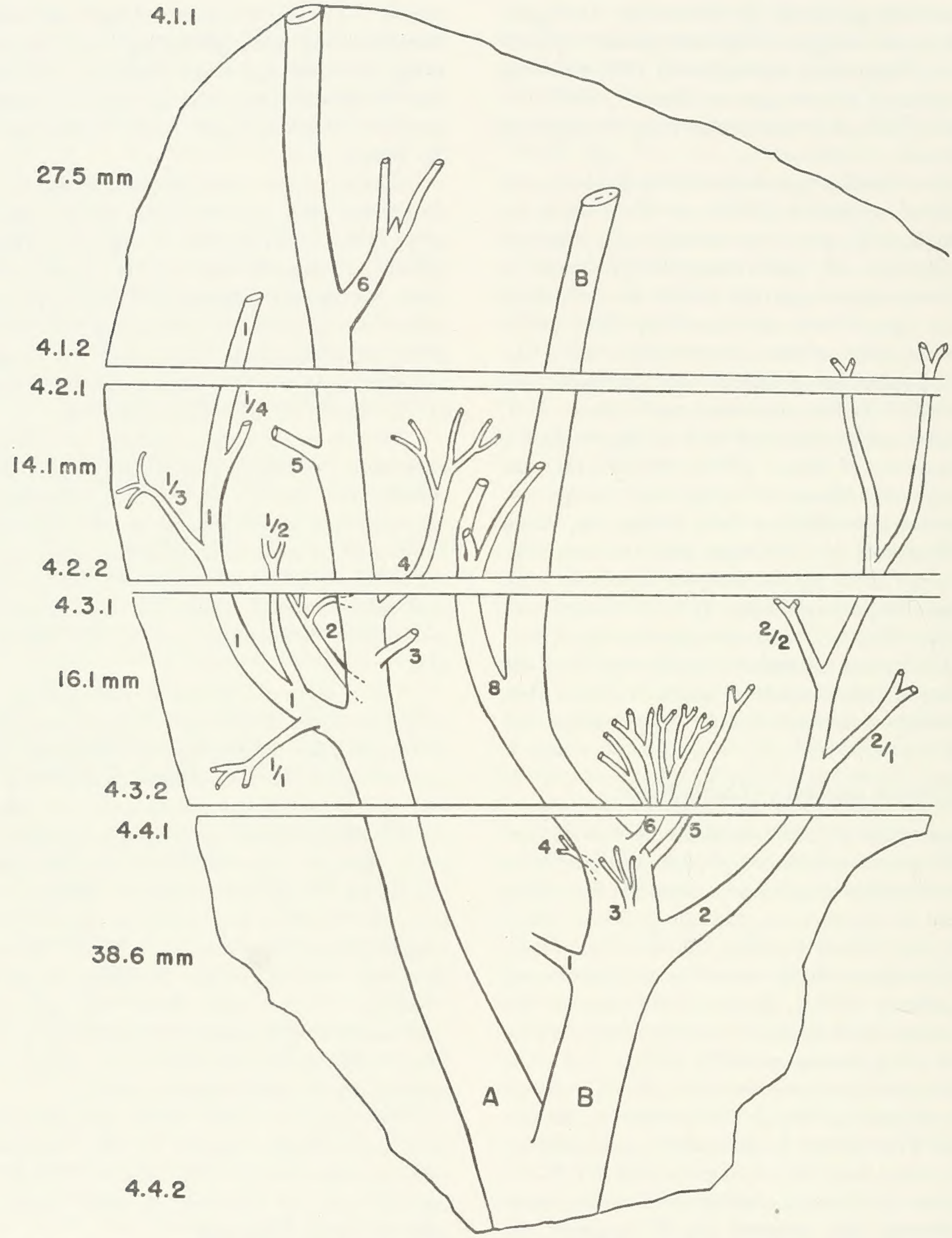
One difference between *P. dawsonii* on the Gaspé and at Abitibi River is the more marked incurving of the latter sporangia. They are also usually filled with spores. The majority of sporangia in the Gaspé specimens are empty. Hence we explain the difference in attitude and content of sporangia as indicative of an age difference, an ontogenetic feature. Streel (personal communication) has seen spores from both Gaspé and Abitibi River material. Without any information about the attitude and apparent age of the sporangia he suggested that the spores from Abitibi River were younger than those from the Gaspé. Therefore, on the reconstruction (Text-fig. 13) we have shown the more terminal fertile branches to have younger, more incurved sporangia (Abitibi River) and the more proximal ones (Gaspé) to be variously disposed, older, and presumably empty.

We regard the Abitibi River collection as providing unusual and striking support for our interpretation of the anatomy, morphology and habit of *Psilophyton dawsonii* that are based on the study of "serial" peels of *P. dawsonii* from the Gaspé Peninsula.

## 3. Vegetative lateral branching system: Douglastown, Gaspé. Specimen: paratype 192

### a. Axis A.

We describe in detail a vegetative branching system



Text-figure 4. A reconstruction of the vegetative branching of *Psilophyton dawsonii* as found in specimen 192 from Gaspé Peninsula. Note the irregular spiral arrangement of the lower branches on both main axes and the alternate, distichous arrangement higher up on the axes. Branches 6 on axis A and 8 on axis B are both believed to be bases of fertile branch systems. Branches are numbered and the order of their subdivisions is indicated by a slash, *e.g.* first branch of branch 1 is 1/1. Thickness of the four blocks is given in millimeters and the numbers of the cut surfaces are indicated on the left. Reconstruction not to scale but approximately × 3.

found in specimen 192 for three reasons. First we have followed the system throughout the specimen. Second the specimen contains the most extensive vegetative system we have found and details of the vegetative branching *Psilophyton* have heretofore been unknown. Third, and most important, it bears the lower parts of fertile branching systems as well as the sterile. Specimen 192 was 10.24 cm in length. It was cut into four pieces (Text-fig. 4). The two main axes referred to as A and B are outlined in the sketch of the specimen.

At the base of the specimen there is a large axis which soon dichotomizes. Each of the axes produced branches so extensively and remains so large that we have designated them A and B in order to describe them separately.

Peels from the base of the specimen show an axis whose stele is in the process of dichotomizing (Text-fig. 5a). The stele in cross section is elongated and has two protoxylem strands. The metaxylem and cortex are identical to the same tissues in axes of the fertile branching system. Somewhat higher the amount of protoxylem is greater and both the stele, and then the axis, dichotomize (Text-fig. 5b-d). From this level onward we shall follow only axis A. Note however that the stele of axis B elongates quickly and soon shows three protoxylem areas (Text-fig. 5d). This demonstrates that axis B will branch soon and at a lower level than axis A.

The stele of axis A remains unchanged for more than 3.5 cm and then begins to branch. The successive lateral branches of axis A are numbered 1-6 (Text-fig. 4). Branchlets produced in turn by them are indicated by a slash, for example 1/1, 1/2, 1/3.

Text-figure 5g, from a higher peel, shows the stele of branch 1 free from that of axis A. It is smaller and is centrarch. The first lateral of branch 1 curves downward. This is demonstrated by the appearance of ultimate sterile tips on the left side of Text-figure 5g. The several branchlets (a, b, c) at the apex of lateral 1/1 are produced by dichotomous divisions. In Text-figures 5h-j the curved stele of branch 1/1 is seen joining the stele of branch 1 which in turn is producing the vascular supply of its second lateral (1/2). In Text-figure 5k the stele of 1/2 is free and axis A has produced the vascular strand for its second lateral branch (2).

In Text-figure 6a axis A is giving rise to a third lateral (3). Meanwhile branch 2 has become free and has produced its first lateral, 2/1 which is bent downward from its insertion on 2. Its attachment to branch 2 will be seen in the next illustration. In subseqeunt peels the xylem of branch 2 dichotomizes, suggesting that it terminated in several small appendages. Branch 1 and its second lateral are both well preserved.

In Text-figure 6b the union of branch 2/1 with its parent 2 shows that the former did in fact bend downward. Axis A and branches 1 and 1/2 have changed little from the previous figure. Branch 3 disappears quickly.

In Text-figure 6c we illustrate only the origin of a fourth lateral from axis A and the diminishing size of branch 2.

Text-figure 6d shows the stele of branch 4 free from the main stele although still within a common cortex. Branch 2 and its ultimate divisions have now terminated.

Text-figure 6e illustrates axis A, its fourth lateral, 4, and the second lateral produced by branch 1 which itself is now producing a third lateral, 1/3.

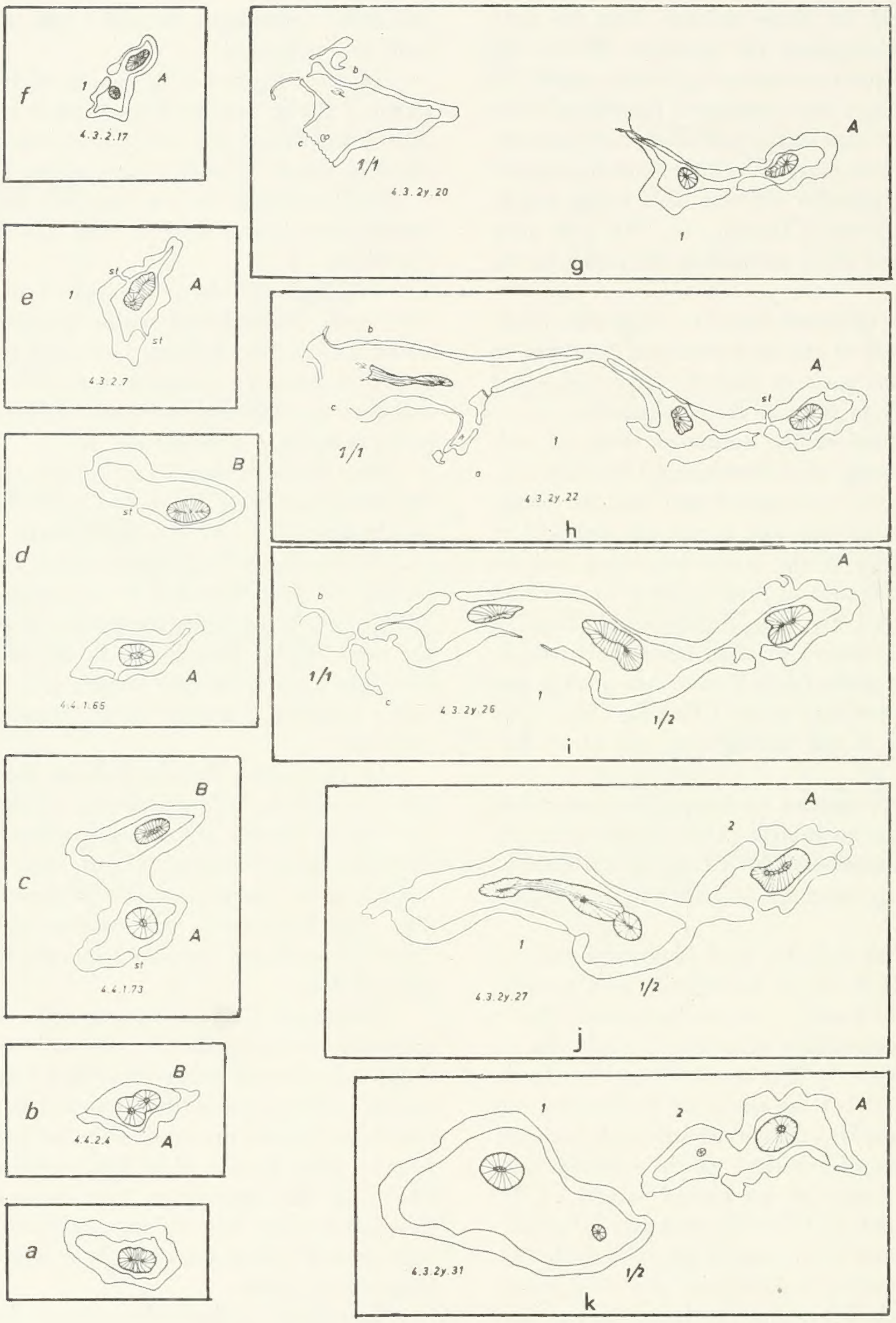
Text-figure 6f shows axis A little changed. Branch 4 is cut obliquely. Trace 1/3 is free from the stele of branch 1 and branch 1/2 is cut at a higher level.

In Text-figure 7a the main axis is unchanged. The third lateral, 1/3, from branch 1 is free and a bundle of a fourth lateral, 1/4, is free from the parent stele but is still within the same cortex. Branch 4 is in the process of rapid division. The stele of its first lateral, 4/1, has already divided and a trace to a second lateral branch has already been produced.

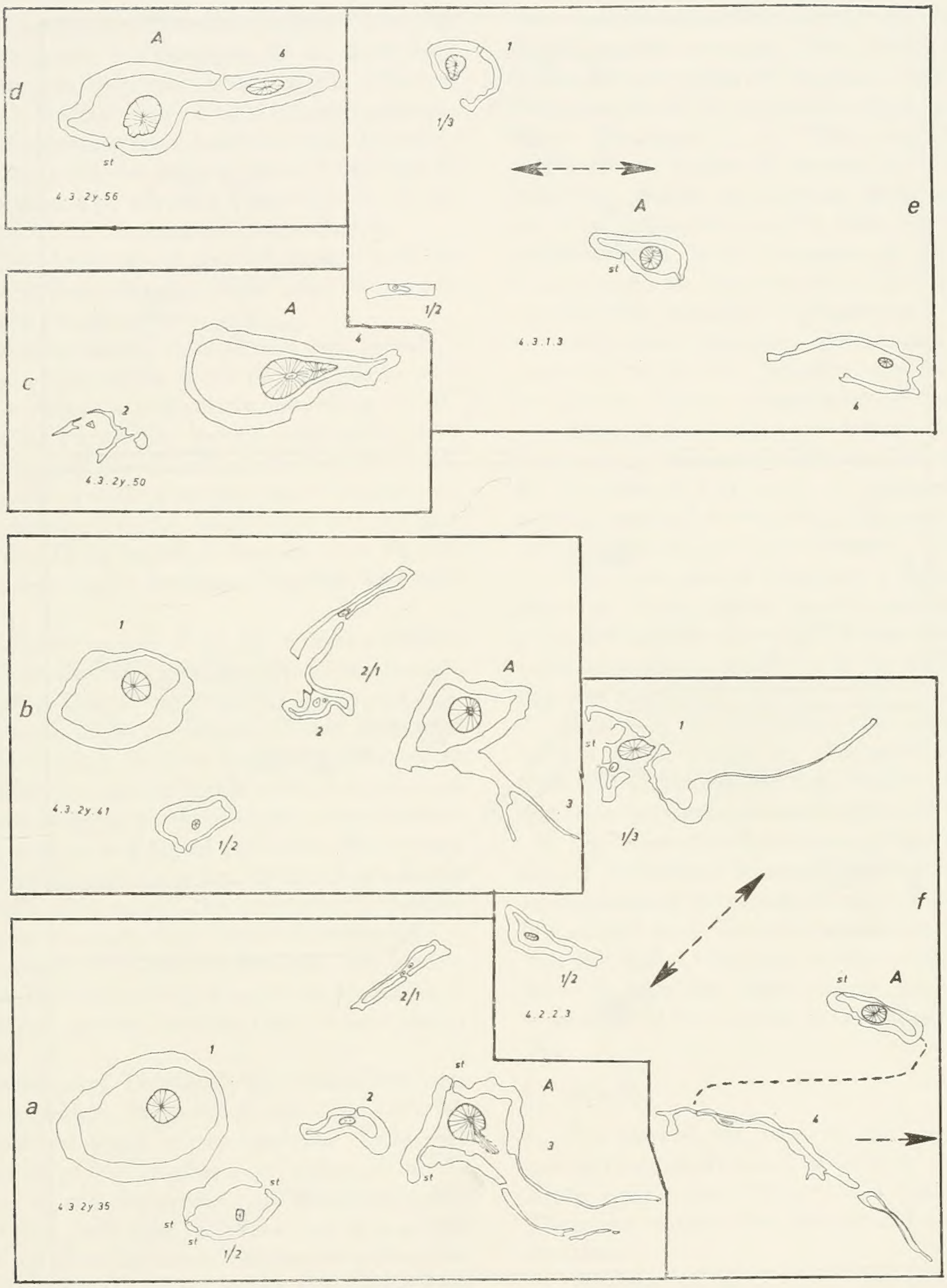
In Text-figure 7b axis A shows the first evidence of a fifth lateral branch. It appears as a bulge on the margin of the xylem. Branch 1/3 is well preserved and the profuse branching of 4 is clearly evident. Branch 4/1 has dichotomized into two small axes. One of these 4/1 b has two bundles. This indicates it will produce still another forking. Branch 4 itself now contains 3 bundles which will supply 4, 4/2 and 4/3.

Text-figure 7c is taken near the termination of the sterile tips of branch 4 and its lesser branchlets. Branch 1/3 shows a division of xylem into three bundles that will soon appear in three sterile tips. Branch 1 is normal. Clearly its fourth lateral was preserved only for a short distance. Axis A and a small portion of its 5th lateral appendage are seen. Obviously this appendage bent downward quickly after its origin because here its stele has been cut twice, once in the cortex of axis A and once above axis A surrounded by a fragment of cortex.

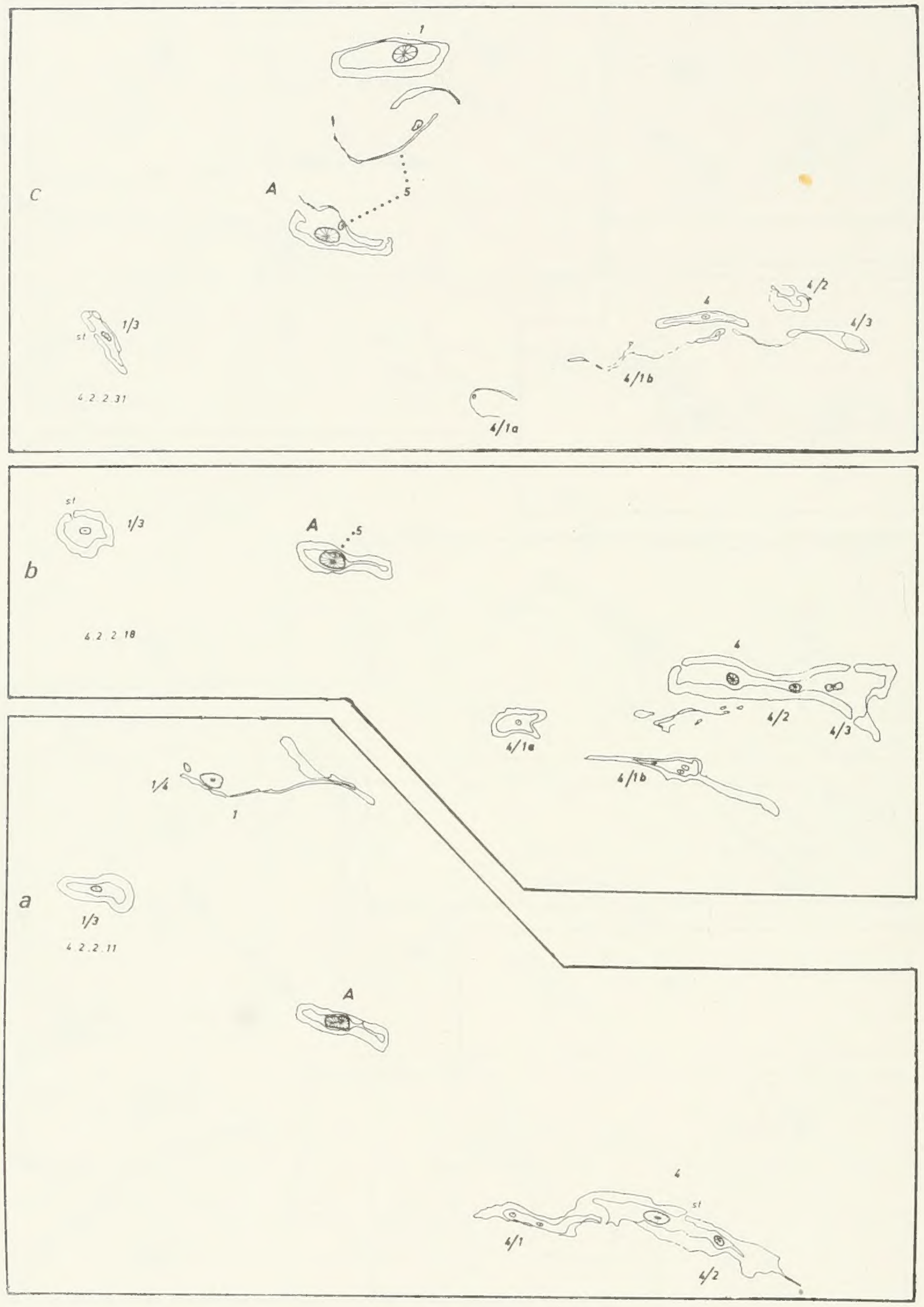
Text-figure 8a shows the union of the downwardly bent branch 5 to its parent axis (A). Branch 1 is well preserved and branch 1/3 shows one of the three xylem groups now free from the other two. The subsequent subdivisions of branch 1/3 are our best example of delicate, recurved or



Text-figures 5-8. Selected peels, taken from base toward apex, illustrating details of vegetative branching of axis A (see Text-fig. 4). Text-fig. 5, a-k, lowest sections. Each diagram bears the number of the peel from which it was made. Numbering on branches is as on Text-figure 4. st — stomate. See also footnote which applies to Text-figures 5-12. Full description in text; × 5.



Text-figure 6. Selected peels, a-f, illustrating details of vegetative branching at a higher level than Text-figure 5. f has been rearranged to fit the page. Description in text. All symbols as on Text-figure 5; × 6.



Text-figure 7. Selected peels, a-c, from levels higher than Text-figure 6. Symbols unchanged. Description in text; × 6.

straight, ultimate, sterile tips. Therefore, we have illustrated several successive peels in Text-figure 8h to show how branch 1/3 terminates in three slender, sterile divisions (1/3a, 1/3b, 1/3c). We believe this kind of branching characterized many of the ultimate divisions of the sterile branches. For example, in this particular series of peels, the endings of the branchlets produced by branch 4 (Text-figs. 7b, c) are the most similar to these terminations of branch 1/3.

Text-figure 8b shows axis A and the beginning of its sixth lateral branch. One sees only a slight bulge on one side of the stele. Branch 1 is still present.

In Text-figure 8c branch A is normal and branch 1 lies near the edge of the cobble, about to disappear outside it. Branch 6 now becomes particularly interesting (Text-fig. 8d) because its bundle has become rectangular, with three protoxylem strands like a bundle at the base of a fertile lateral branch system. For the first time axis A has behaved like a main axis bearing a fertile branch. Like a fertile axis, the rectangular bundle of branch 6 becomes three by two successive, close dichotomies (compare Text-figs. 8d-f with Text-figs. 3j, k).

Text-figure 8f shows axis A in the normal condition between branchings. Branch 6 now consists of three branchlets (6/1, 6/2, 6/3). The central branchlet is tiny and is in the process of aborting. The resemblance of this illustration to Text-figure 3k which is the first double dichotomy of an axis with attached sporangia (a fertile axis) is quickly apparent. It is most unfortunate that branch 6 now runs out of the specimen and can be followed no further. We are convinced however that branch 6 is in fact the first fertile lateral branch to be produced by axis A. Our conviction is based on the observation of this pattern of branching repeatedly in fertile branch systems of *Psilophyton dawsonii.* The branching illustrated in Text-figures 3i-m drawn from specimens 31 and 35 represents the pattern we have found to be constant in our specimens.

The final illustration, Text-figure 8g, is made from near the apex of the specimen. Only axis A which has been followed throughout the length of the specimen (10.24 cm) remains. Almost all of its branches were broken off at the time of breaking up and displacement of the masses of clay that contained the plant axes. However axis A was still vigorous at the top of the specimen. Its elongate protoxylem indicates the beginning of another branch that would have appeared at a higher level.

SUMMARY of branching of sterile axis A (Text-fig. 4, 13).

At the base of specimen 192 a typical centrarch xylem strand dichotomizes. One axis, A, then soon produces four laterals in quick succession. Their precise arrangement is uncertain but they appear to be spiral. This may be related to the production of an unusually large central mass of protoxylem (Text-figs. 5d, e). This protoxylem condition is found only in regions of profuse and somewhat irregular branching. Higher up, alternate distichous branching appears as branches 5, 6 and a trace for 7 are produced at wider intervals. This arrangement is the one found in all of our specimens that contain only lateral fertile branch systems with sporangia in attachment. It is also typical of the compression specimens from Abitibi River that were uncovered by Hueber. Alternate, distichous branching also characterizes branch 1 which produces four laterals.

Interestingly, the first six branches of axis A are unequal in vigor. Branches 1 and 6 are both more vigorous than 2-5. Branches 2, 3, 4 and 5 are comparable in size to the laterals produced by branch 1 whereas branches 1 and 6 are more like major branch systems.

The sixth branch from axis A gives strong evidence that it is a fertile lateral axis. We were able to follow it up to its first double dichotomy. At this level one of its three branchlets aborts, exactly as in the fertile systems (Text-figs. 8d-f and 3j, k).

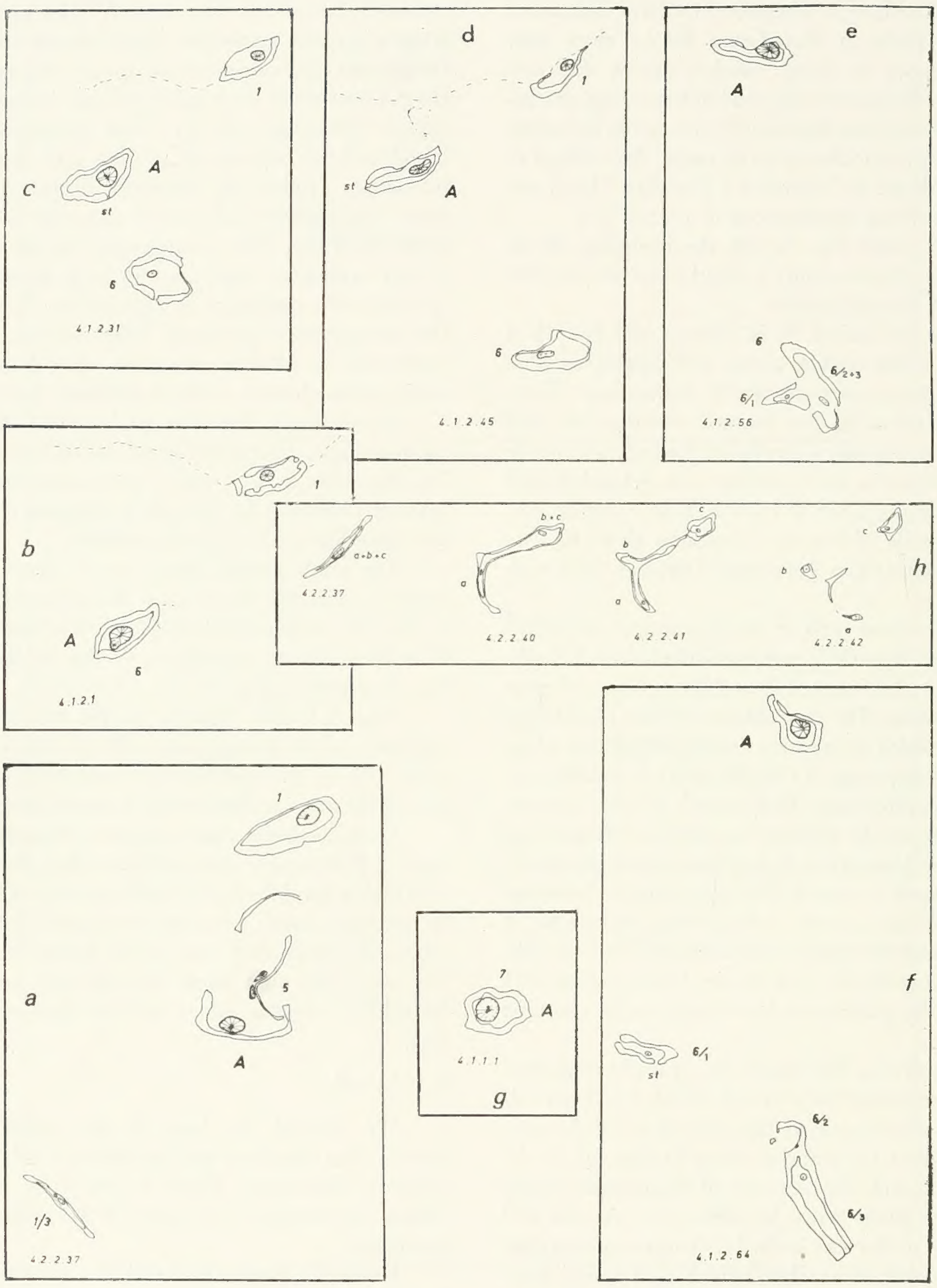
Axis A is still vigorous as the top of the specimen is reached and its protoxylem indicates the production of another (7) on the opposite side from branch 6, the alternate distichous arrangement which is usual for fertile branches.

We believe the above sequence demonstrates that large axes of *Psilophyton dawsonii* branched dichotomously, that at a higher level they produced a system of irregularly spirally arranged sterile branches terminated by sterile tips, and that still higher they bore fertile lateral branching systems. We note also that some laterals are more vigorous and branchlike whereas others are less vigorous and more leaflike.

b. Axis B.

We showed the base of the sterile branching system in Text-figs. 5a-d and we followed axis B to a level just above a dichotomy. There it had three protoxylem areas. These demonstrate that axis B will soon produce lateral branches.

However, above this level, the xylem strand of axis B is suddenly absent and only fragments of its cortex remain. This situation is found in peels made over a distance of 4 mm. Then suddenly we find a naked stele with three protoxylem strands exactly like the stele seen below. Slightly higher in the specimen this naked stele is again surrounded



Text-figure 8. Selected peels, a-g, at a still higher level. Symbols unchanged. Description in text. Figure h shows several sections to illustrate the termination of a vegetative branchlet in three delicate apices; × 6.

by normal cortex and the branch is again intact. We believe axis B was damaged and its stele broken but that it was held almost in place by the enclosing calcareous mud.

Text-figure 9a shows axis B above the break. It has three protoxylem strands. Higher up the stele is enlarged and the two lateral protoxylem strands become unequally distant from the central one. This is the first indication of a succession of lateral branches. Some of the fragments of cortex out of which the stele of axis B slipped are also shown.

In Text-figure 9b the origin of branch 1 is clearly visible as a large bulge on the left side of the xylem strand. The protoxylem of branch 2 is distinct on the opposite side of the stele.

Text-figure 9c shows stele B now surrounded by a considerable amount of broken cortex. Branches 1 and 2 are represented by xylem strands still enclosed in the cortex of axis B.

In Text-figure 9d the first lateral, 1, is seen to be completely free. It consists of a small, terete bundle and a narrow, broken cortex. Branch 2 is attached to the axis at an obtuse angle and therefore it appears, still connected, in several subsequent peels. The stele of axis B shows another bulge but one that is different from the usual type of emission of lateral bundles. The explanation will soon be apparent. At the same time the central group of protoxylem cells begins to be enlarged as shown by crosshatching.

Text-figure 9e shows the beginning of a profuse branching of the stele of axis B, and the starting point of a new behavior of the stele. Five branches (No. 3, 4, 5, 6, 7) of different sizes are produced in the vertical distance of only 2.5 mm. Here branches 1 and 2 are little changed. Axis B shows another new lateral trace, 3, which will be free slightly higher up. The stele of axis B elongates. Both its central area of protoxylem and its metaxylem are much enlarged (Pl. 24, fig. 68). For convenience we refer to this entire mass as B although very soon B and a cluster of branches will be separated out of the mass.

In Text-figure 9f, 10 and Plate 24, figs. 62-65 the striking features shown are the changes in size, form and structure of the stele of branch 3 which is enlarged. The stele is characterized by the enlargement of the central area of protoxylem, without the addition of parenchyma, surrounded by a peripheral zone consisting of large tracheids. Several small traces in the cortex arose by dichotomous divisions, an unusual origin when compared with branches 2 and 8 on Axis B and with branches 1, 4, 6 of axis A. On the side of the stele opposite branch 3 a bulge in the main stele represents part of the xylem of branch 4. The xylem strand of 4 apparently arched upward and then recurved. Evidence for this statement is provided by the trace of branch 4 that has been cut near the margin of the stem. Further evidence is the small strand of xylem that extends out of the main mass of xylem toward branch 4 (see Text-fig. 9g). Branch 4 is remarkably similar to 3. Both give rise to a cluster of tiny branchlets. Branches 1 and 2 in Text-figure 9f are little changed.

Particularly interesting at this point are Text-figures 9f, g, 10a, b, and Plate 24, fig. 63 because the massive xylem enlarges in a peculiar manner. Axis B is obviously bending to the left and is cut obliquely. Thus the xylem looks abnormally large. In addition the profusion of branches produced in a short vertical distance means that the large mass of xylem consists of the vascular strands of a number of branches. If this mass could be seen in three dimensions, it would be a compact mass with protuberances on all sides.

Text-figure 10a, Plate 24, fig. 63, show two new lateral bulges in the stele of axis B. They are numbered 5 and 6. Branch 5 already has its own centrarch protoxylem. Branches 3 and 4 are small and inconspicuous as is shown by the course of their bundles in Text-figures 10a-e. The curved mass of xylem of axis B is cut tangentially and is further attenuated.

Text-figure 10b shows the final separation of the bundles that comprised the large xylem mass called B up until this level. The strands to branches 4 and 5 are still in contact and a new trace has become obvious, trace 7. The xylem strand to branch 6 is apparent on the side of the stele of axis B. Branchlets from 3 are still attached to the axis.

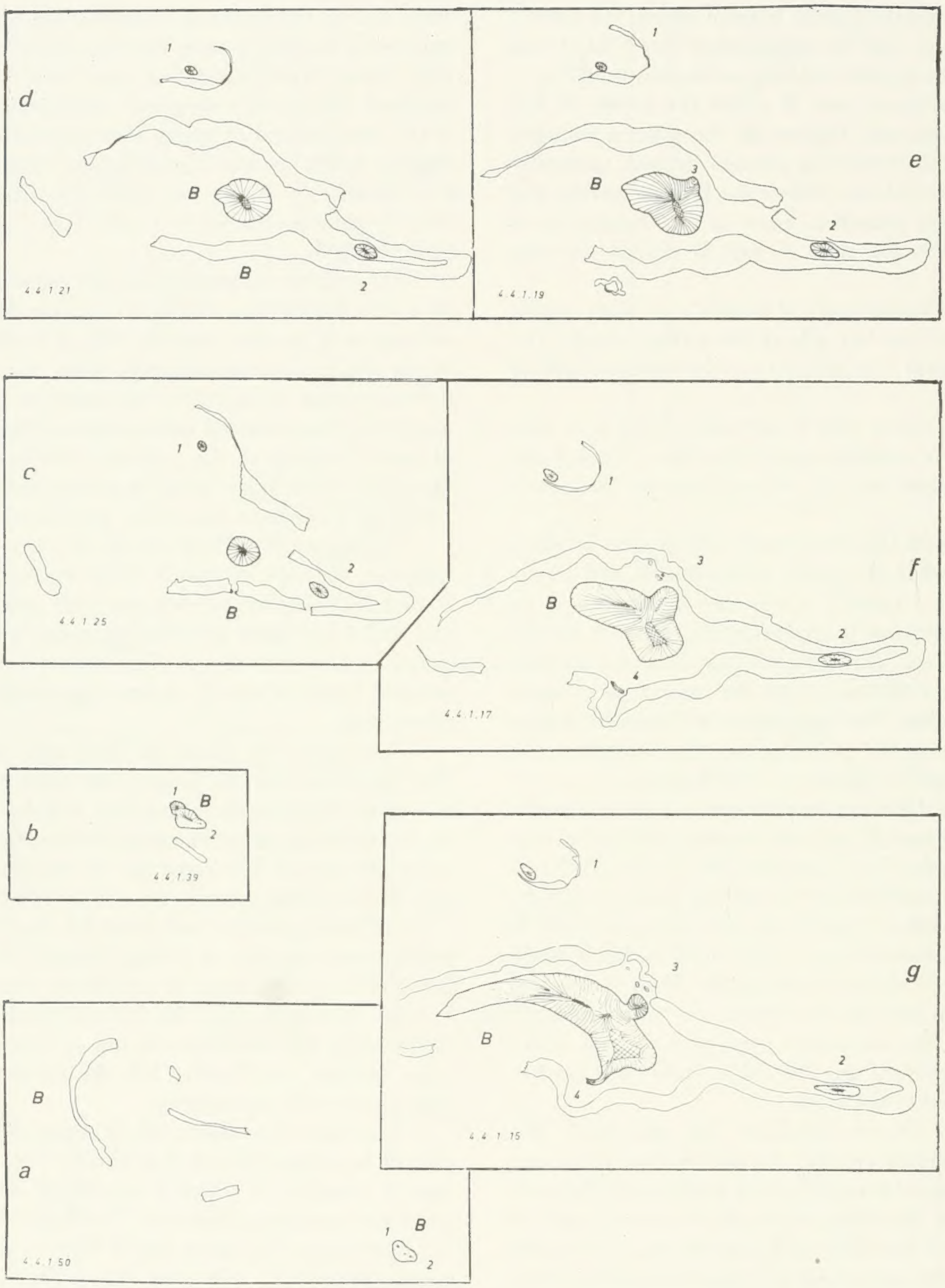
In Text-figure 10c, and Plate 24, fig. 62 nearly all the branch traces are free in a large cortical enclosure and axis B, which is upright again, is cut almost transversely.

In Text-figure 10d the insignificance of branch 7 is indicated by the diminution in size of its trace which terminates without ever having left the parent axis. All other branches are self-explanatory.

Text-figure 10e shows axis B separated from the complex of branches. Branch 2 is finally free from its parent axis B. Branches 5, 6 and 3 are still in attachment. Their steles are unequal in diameter; 5 is larger than the others.

Text-figure 11a shows axis B with its single protoxylem strand. Branches 5 and 6 are almost free from each other. Branch 2 continues vigorously while branch 3 ends in at least three small branchlets. From the above series it is evident that branches 3 and 4 terminated rapidly.

Text-figure 11b shows the stele of axis B in its more nor-



Text-figures 9-12. Selected peels, taken from base toward apex, illustrating details of branching of axis B (see Text-fig. 4). Text-figure 9, a-g, showing especially the enlargement of protoxylem (cross hatched) and metaxylem (lined) below region of profuse vegetative branching. Symbols unchanged, description in text; × 6.

mal condition about to produce a branch on one side. Branch 2 is vigorous. Branches 5 and 6 are now separated. Branch 3 is about to end.

Text-figure 11c shows axis B about to produce another trace that will be the vascular supply in branch 8. Branch 5 is reduced in size. Branch 2 is producing a small lateral which is cut obliquely. Branch 6 has subdivided at least three or four times into a tangle of small branchlets.

Before beginning the description of Text-figure 12 it is necessary to remark that the distance between the branches on the peels have become too great to continue illustrating them in their correct relationship to one another. We have therefore drawn the branches on Text-fig. 12 much closer together than they occur on the peel.

Text-figure 12a, Plate 24, fig. 66 show axis B with another alternate, lateral trace, 8. Two remnants of profusely branched 6 are still present but disappear shortly. Branch 5 is little changed. The xylem of branch 2 has produced a trace, 2/2, which is free. The first lateral of 2, 2/1, has now two traces following a dichotomy. Branch 2 produces a third lateral at a higher level. All of its lateral branches, 2/1, 2/2, 2/3 and branch 2 itself dichotomize once and then disappear. Therefore, we shall not illustrate the branch 2 complex again above the level of Text-figure 12a.

We shall now follow only axis B and its eighth lateral because 8 is certainly the most significant branch that axis B has produced.

Text-figure 12b, Plate 24, fig. 67 were selected to show branch 8 in the course of division into three branchlets by a pair of closely spaced dichotomies. One small trace is already free (the first dichotomy) but the other two traces are not yet separated. All are included in the same cortex. The outline of this xylem group is rectangular (more obvious at a lower level). This is the first emission of a rectangular trace by axis B. It recalls the rectangular bundle which identified branch 6 of axis A as a fertile lateral branch.

Text-figure 12c shows axis B and the three branches produced by the double dichotomy of its branch 8 (8/1, 8/2, 8/3). Of these three branchlets, 8/1 aborts, 8/3 runs out of the nodule, and 8/2 is seen in the next figure.

In Text-figure 12d axis B shows evidence of a ninth branch, to be produced alternately and distichously. Branch 8/2 has divided a second time by a double dichotomy. Its three bundles should soon be found in three new branchlets. This second double dichotomy repeats exactly the pattern we described as typical for fertile branching systems.

Text-figure 12e shows axis B still vigorous at the very apex of the nodule. No other branches are preserved at this level. The trace to lateral branch 9 is nearly free.

SUMMARY of branching of sterile axis B (Text-figs. 4, 13).

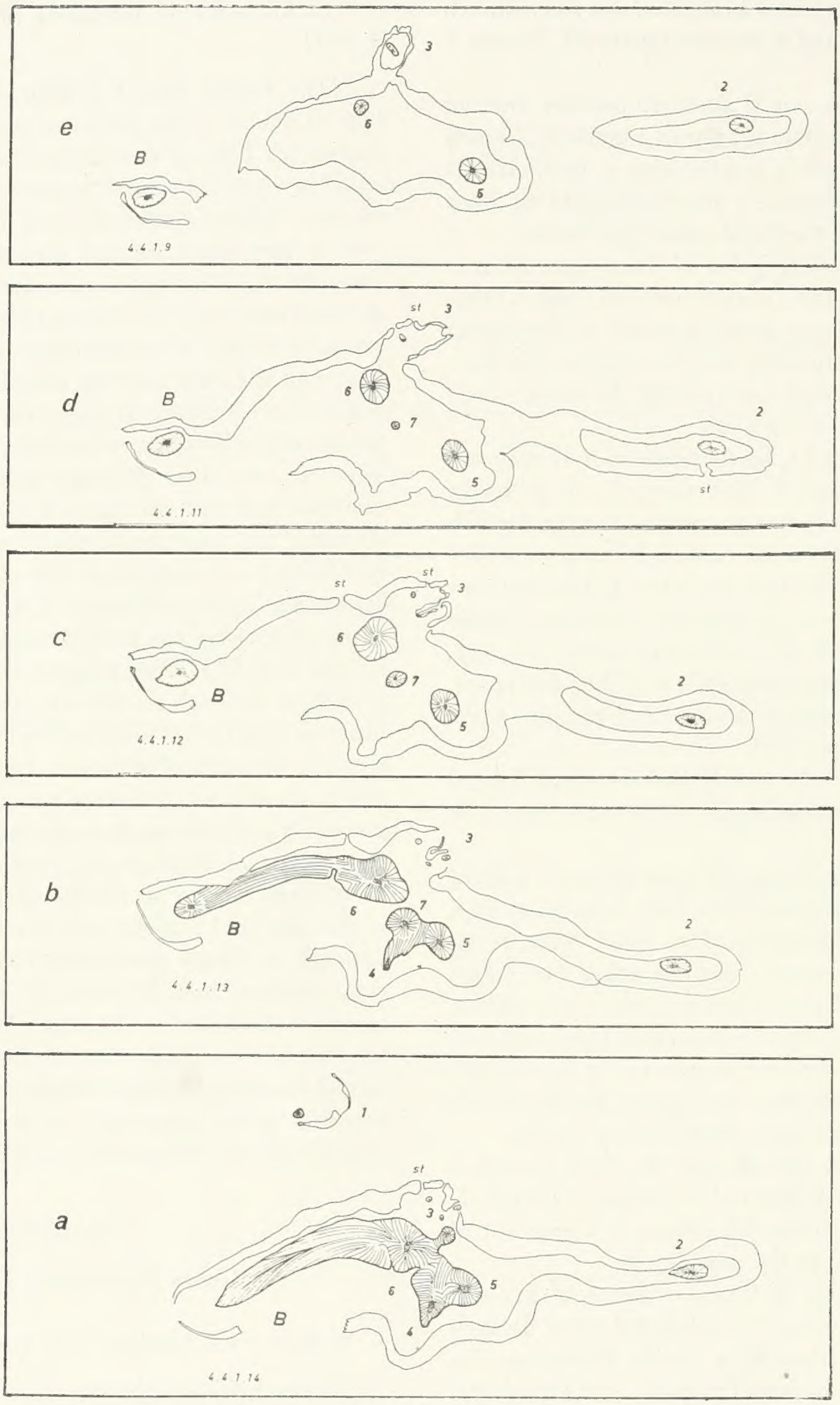
The second branch produced by a dichotomy at the base of cobble 4 also produces laterals spirally and in rapid succession. Like axis A the laterals produced by B are unequal in vigor. The small branches 3, 4, 5, and 6 were given off in a different manner from branches 1, 2, and 8 and over a very short vertical distance, 2.5 mm. At the same time the stele increased considerably in size, and became differentiated into two distinct tissue masses, a large central protoxylem and a surrounding metaxylem. This local behavior of the stele and the meaning of the lateral organs is not easy to elucidate. It might be presumed that they represented a first attempt to evolve a new function, *e.g.* that of adventitious roots, although their anatomy and mode of emission had not yet reached that of a true root. The behavior of the stele recalls that described by Benson (1911) in *Botryopteris antiqua* in the region of adventitious root formation. Thus these organs 3, 4, 5, 6 suggest another hypothesis just as did the small branchlet 1/3 on Axis A (Text-fig. 8a and 8h). We assigned a leaflike function to that branchlet although its delicate, terete, recurved or straight, ultimate tips had evolved neither the dorsiventral organization nor the expanded lamina typical of a leaf. Branches 2 and 8 are like major branch systems, one sterile, one fertile. Branch 8 is preserved through two double dichotomies that resemble in all respects the branching at the base of a fertile system. Higher up the vascular supply of a ninth branch is alternate and distichous as in our typical fertile branching systems in Gaspé specimens 190, 191 and Abitibi River compressions. Axis B is just as vigorous at the top of the specimen as it was at the base. Axis B tells the same story as Axis A, vegetative lateral branches below and fertile lateral branching systems above, and among the vegetative branches some suggesting the origin of leaves and others which might be interpreted as simulating adventitious roots.

## DIAGNOSIS

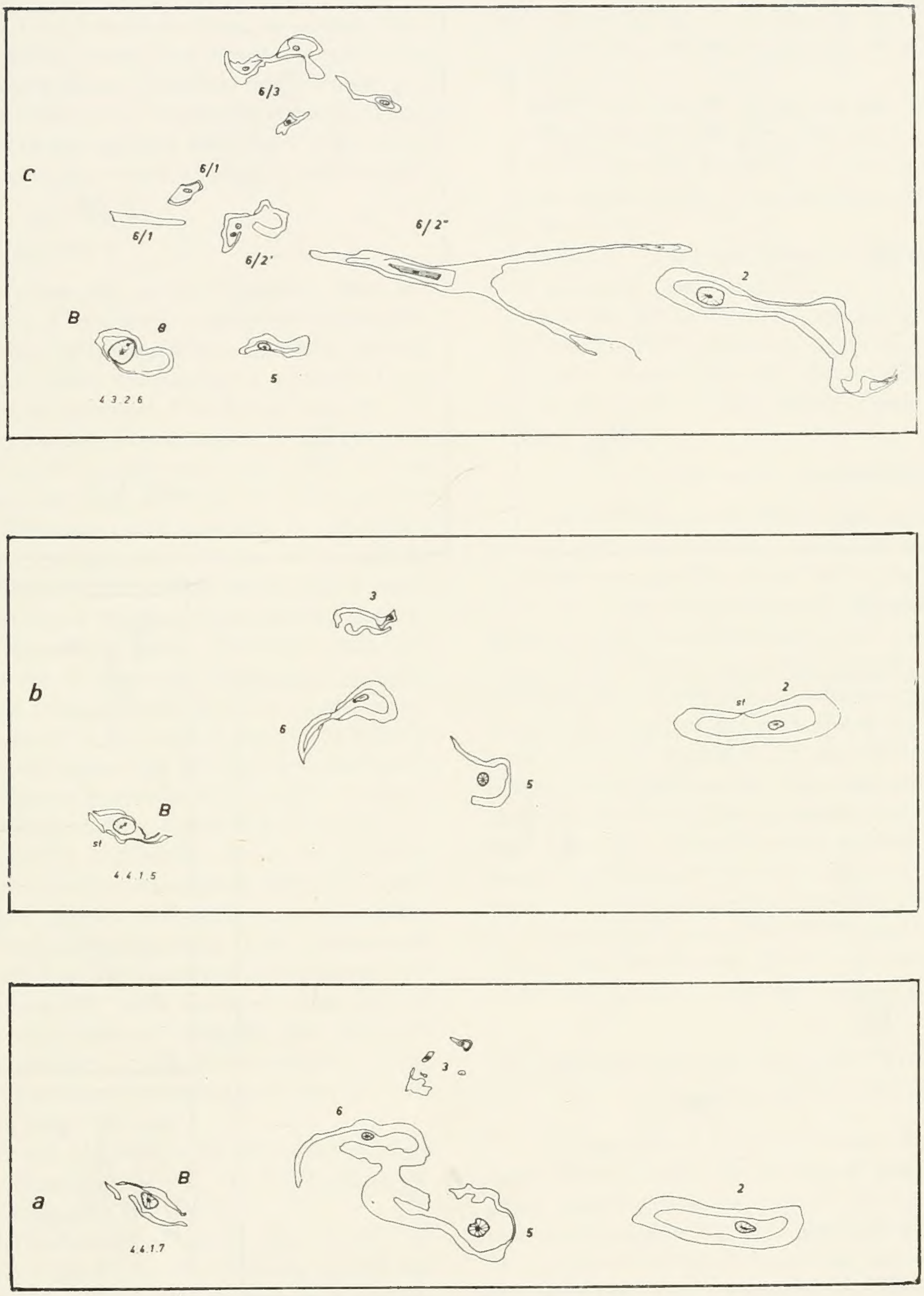
### Genus *Psilophyton* Dawson, 1859

Diagnosis of Hueber, 1968, emended.

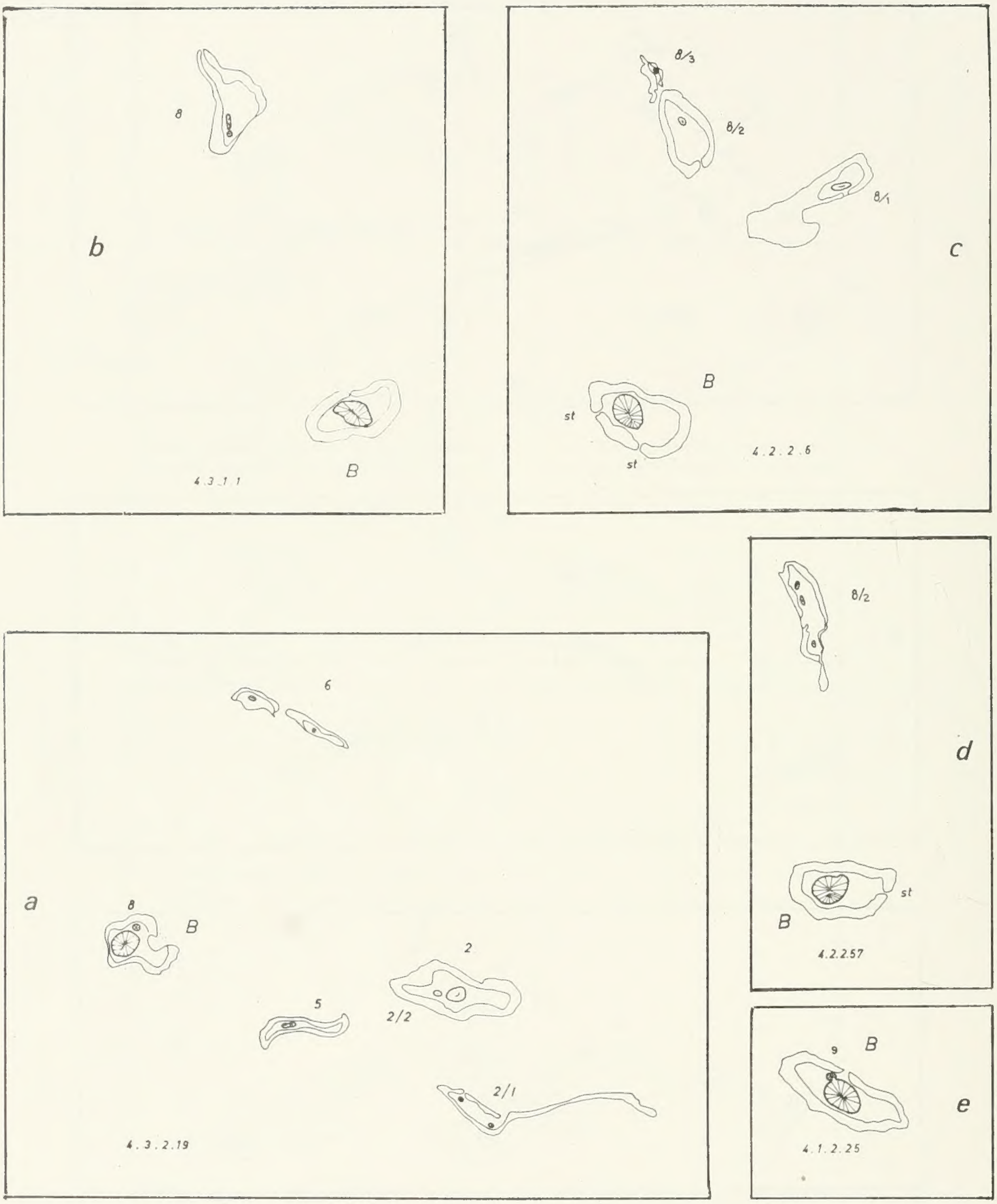
Stems branch dichotomously and laterally, the latter in an irregular, close spiral in zones of vegetative branching; fertile branches, in zones alternating with vegetative zones, more distant and alternate, distichous; lateral branches themselves branch either laterally or dichotomously with successive dichotomies each formed at right angles to the



Text-figure 10. Selected peels, a-e, of levels above Text-fig. 9. All symbols unchanged. Description in text; × 6.



Text-figure 11. Selected peels, a-c, of levels above Text-figure 10. Symbols unchanged. Description in text; × 6.



Text-figure 12. Selected peels, a-e, of still higher levels of vegetative branching. Symbols unchanged. Description in text; × 6.

other; axes naked or spinous, ridged or unridged, compressions may be marked by punctiform scars; sporangia elongate-elliptical, pendulous, paired, and borne terminally on repeatedly dichotomized lateral branches, total number per lateral branch large; dehiscence longitudinal along facing surfaces of paired sporangia; xylem a solid strand, centrarch; outer cortex collenchymatous except in areas of substomatal chambers.

Species *P. dawsonii,* sp. nov.

Characteristics as for the genus. Vegetative branches three-dimensional and of two sizes; terminated by slender, blunt tips in various attitudes; fertile branches usually dichotomize six times before terminating in clusters of approximately 32 pairs of sporangia 3.0-5.0 mm long by 1.0-1.5 mm in diameter, sporangial wall similar to stem cortex; at maturity consisting of an outer carbonized layer and an inner cellular membrane; both abortions of sporangia and of limbs of some dichotomies cause variations in total number; each of the first two apparent dichotomies is actually two closely spaced dichotomies each of which should result in three branches but one of the three aborts leaving a stump between the two remaining limbs. Protostele relatively large, ¼ the diameter of the stem; centrarch; becoming massive with several enlarged protoxylem areas and many radially aligned tracheids at the level of vegetative branching; in the area of fertile branching protoxylem branches alternately and distichously foreshadowing a similar arrangement of lateral branches; trace to fertile branch at first terete, soon characteristically rectangular; xylem all tracheids, scalariform pitted to modified scalariform resembling rudimentary circular pits; phloem and inner cortex parenchymatous, outer cortex collenchymatous with substomatal chambers; epidermis of small boxshaped cells; spores, 40-75 $\mu$ in diameter, smooth, with darkened areas around commissures, curvaturae; spores resemble the dispersed spore genera *Retusotriletes* or *Phyllothecotriletes;* young spores surrounded by a minutely ornamented layer (? perispore) which breaks away with age.

Holotypes: Cornell University Paleobotanical Collection Number 190, Plate 20, figs. 30, 31, 33-37; Plate 21, figs. 38, 39; Plate 24, fig. 69 (loc. No. 31).

Paratypes: CUPC No. 191, Plate 18, figs. 11, 17, 18; Plate 19, figs. 27, 28; Plate 20, fig. 32; Plate 21, figs. 40, 41; Plate 22, fig. 43 (loc. No. 35); CUPC No. 192, Plate 17, figs. 5, 6; Plate 18, figs. 12-14; Plate 19, figs. 19, 20, 22, 25, 26; Plate 24, figs. 62-68 (loc. No. 4).

CUPC No. 193, Pl. 22, fig. 50; Pl. 23, figs. 54, 55.

CUPC No. 194, Pl. 18, fig. 16; Plate 19, fig. 24; Pl. 20, fig. 29; Plate 22, figs. 42, 49 (loc. No. 13).

CUPC No. 195, Pl. 19, fig. 21; Pl. 23, figs. 56-61 (loc. No. 21).

CUPC No. 196, Pl. 22, fig. 48 (loc. No. 23).

CUPC No. 197, Pl. 19, fig. 23 (loc. No. 32).

CUPC No. 198, Pl. 18, fig. 15 (loc. No. 34).

Geological Survey of Canada No. 32719, Pl. 17, fig. 2 (loc. No. 6435).

GSC No. 32720 and slides a-e, Plate 17, figs. 3, 7-10; Plate 23, fig. 51 (loc. No. 6435).

GSC No. 32721, Plate 23, fig. 52 (loc. No. 6435).

GSC No. 32722, Plate 23, fig. 53 (loc. No. 6435).

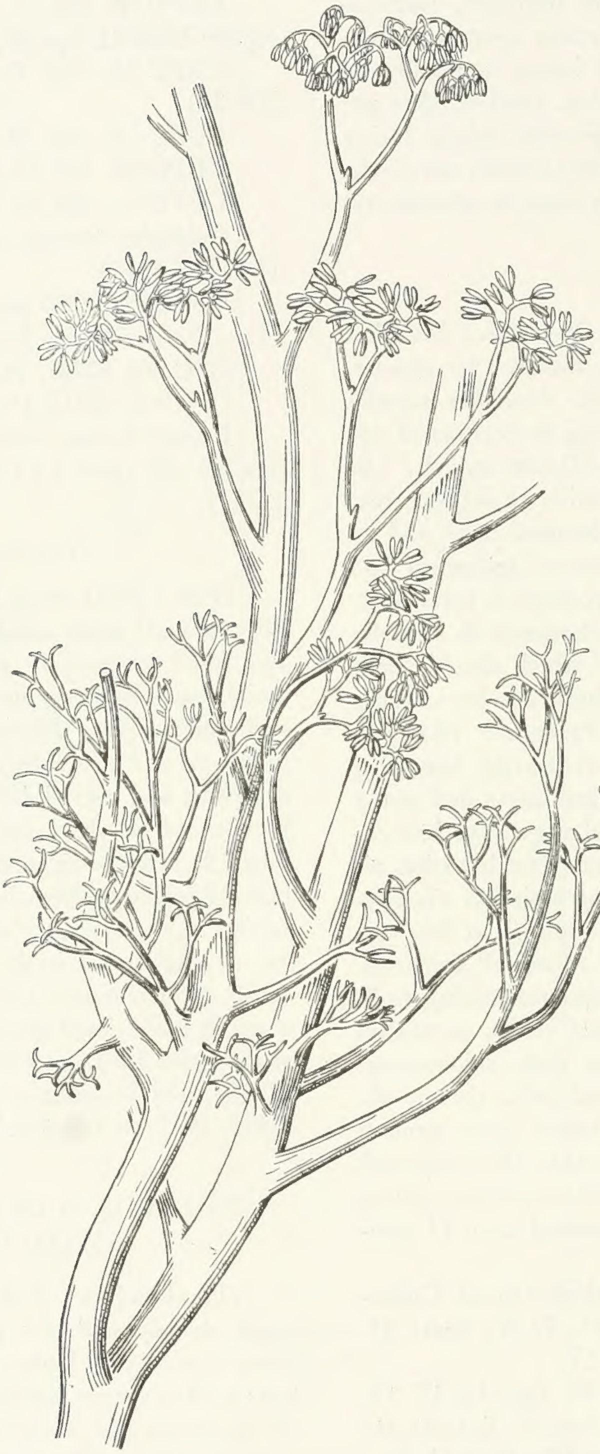
United States National Museum No. 175772, Pl. 22, figs. 44, 45 (peel 1.1.1.2), 46, 47 (peel 1.1.1.1) (loc. No. 14251).

### THE NAME *DAWSONITES*

Halle (1916) erected *Dawsonites,* as a provisional name for use until some worker discovered the true affinity of any fossil temporarily placed in it. He described his material as: "Sporangium-bearing branch-systems, dividing dichotomously, or differentiated into a sympodially formed main axis and bifurcating lateral branches. Ultimate branches slender and curved, bearing terminal capsules of a narrowly obovoid or short fusiform shape and usually 3-5 mm long." It is now demonstrated that *Psilophyton* was a plant bearing fertile systems like those described by Halle. *Dawsonites* is, therefore, to be maintained as a form genus when only a portion of a fertile system is found, and it can not be shown by techniques to be *Psilophyton.* We would use the name in a restricted sense as intended by Halle (1916) and as discussed by Lang (1931, 1932), and by Croft and Lang (1942), and Stockmans (1940), and not as used by Høeg (1935, 1967) and Kräusel and Weyland (1933, 1935).

## COMPARISON OF *PSILOPHYTON DAWSONII* WITH OTHER SPECIES

The abundance of detail revealed by *P. dawsonii* contrasts sharply with the paucity of data for other species. Some anatomy is known for *P. princeps* (Hueber, 1968), but no other species has been described with the combination of vegetative and fertile branching and anatomy. The most extensive taxonomic treatment of *Psilophyton* and associated plants (Høeg, 1967 *in* Boureau's Traité) confuses *Psilophyton* and *Sawdonia* (*P. princeps* var. *ornatum*) although Høeg obviously recognized the need for a complete



Text-figure 13. Reconstruction of plant of *Psilophyton dawsonii* based on calcareous petrifactions from Gaspé Peninsula and compressions from Abitibi River, Ontario. Vegetative branching, irregularly spiral, shown below, fertile branching, alternate and distichous, shown above. Some branchlets reduced and simulating small but unplanated leaves; some branches more indefinite in length. Older sporangia shown more spread out, younger more incurved. First two "double dichotomies" of fertile branches indicated by aborted stumps in angle of apparent single dichotomies.

taxonomic revision of these early plants that bore either terminal or lateral sporangia. Høeg's figures 196, 198-201, 207-209 are now recognized as *Sawdonia,* not *Psilophyton.* His figures 238-241 of *Dawsonites* illustrate *Psilophyton*-like fertile branches. Other species of *Dawsonites* in Høeg's survey do not, in our opinion, conform to Halle's definition of the genus. It is also possible, in view of the vegetative branching of our new *P. dawsonii,* that *Psilodendrion* (Høeg, 1967, pp. 315-317) might be a species of *Psilophyton* if it were better understood.

*P. dawsonii* can be distinguished from *P. princeps* by its lack of cup-tipped spines, by its vegetative branching and by the size of its sporangia 3.0-5.0 X 1.0-1.5 mm *vs.* 7.5-8.0 X 1.0-2.0. Sporangia of *P. dawsonii* are larger than those of *P. kräuselii* which measure only 2.0-2.5 X 0.5-0.6 mm and the latter species is hairy whereas *P. dawsonii* is glabrous. Vegetative branching of *P. kräuselii* is not known.

The other species of *Psilophyton* for which the sporangia are perhaps known is *P. forbesii* (Andrews, Kasper, and Mencher, 1968). Both vegetative and fertile branches have been found and although the authors are uncertain of the point of attachment of the fertile, they reconstruct the plant with alternating vegetative and fertile regions. Should this interpretation prove to be correct then it is a growth habit with which *P. dawsonii* agrees. Both species are glabrous. *P. forbesii* is known only as compressions and in the abscence of any anatomical structure or detail of the branching of fertile shoots and the number of sporangia they bear, we have no hesitation in designating our material as a new species.

*Psilophyton arcticum* and *P. rectissimum* (Høeg, 1967) are based on sterile material and are represented only by compressions. Both are spiny whereas *P. dawsonii* is glabrous. Whether the fertile parts and the anatomy of these two species if found would prove them to belong to the now more clearly defined *Psilophyton* is uncertain.

Despite the ease and certainty with which *P. dawsonii* can be distinguished from *P. princeps,* there are major similarities. Stems of both species can branch dichotomously. Fertile branches of both are produced alternately and distichously and branch dichotomously about six times before ending in a large number of paired terminal sporangia. Dehiscence in both is longitudinal along facing surfaces. Sporangia of both consist of an outer carbonized wall and an inner, separate membrane that resists oxidative maceration. So far as can be determined the protostele of *P. princeps* is like that of *P. dawsonii* though badly preserved. Collenchymatous cortex and substomatal chambers probably characterize both species. There is little question that the two are natural members of one natural genus.

Now that we begin to understand Dawson's genus, it is interesting to note some of his unrecognized accomplishments. His description (1859) of the "fructification probably in lateral masses, protected by leafy bracts" has long been considered worthless (see Text-fig. 1e). For example Halle (1916, p. 15) called it an "obscure object". However these "obscure objects" are clusters of detached terminal sporangia of *Psilophyton* (Hueber and Banks, 1967, fig. 10; Hueber, 1968, figs. 16, 17). Similarly Dawson's various fragmentary descriptions of the anatomy of *Psilophyton* were discounted because they came from detached specimens of axis. Knowledge of the anatomy of our more complete specimens permitted a search for microscopic preparations made by Dawson and a study of them. Eight slides were found in the General Botany Laboratory at McGill University. They were repolished and covered at the National Mus. Nat. Hist. (U.S. National Museum). They now bear Redpath Museum number 12.534-Slides 1-8. They were made from specimens similar to our calcareous cobbles and the cortex they reveal is like that which we have found. Seven slides show apparent scalariform tracheids (as Dawson reported) but also circular, pitlike areas between the scalariform bars (not reported by Dawson), just as we have described them in our new material. One slide was illustrated in Hueber and Banks (1967, fig. 11). It should be emphasized that to date only normal scalariform tracheids have been found in *Sawdonia* (Hueber and Banks, 1967; Hueber, 1971).

*Psilophyton goldschmidtii* Halle (1916) requires special consideration because Halle carefully segregated several associated but unattached plants into the individual genera *Psilophyton, Dawsonites* Halle, 1916, *Aphyllopteris,* and *Hostinella* even though he believed some of them might be parts of one plant. The stem of *P. goldschmidtii* bore lateral branches which dichotomized repeatedly at a wide angle and apparently always in one plane. The stems were spiny and basal parts of the lateral branches bore occasional spines. If this description is fully correct and if the species is ever found to bear fertile branches with terminal sporangia or to have *Psilophyton* anatomy, then *P. goldschmidtii* is clearly distinct from the several species described above. As yet it has neither sporangia nor anatomy nor is it proven that its lateral branches were flattened into a two-dimensional system.

The *Hostinella* described by Halle varied widely. Some specimens Halle considered identical to lateral branches but because they were glabrous he cautiously excluded them from *Psilophyton*. However Banks (1968a) found a centrarch xylem strand and tracheids identical to those of *P. dawsonii* in a *Hostinella* collected by O. Selling at Röragen, Norway where Halle had collected. This suggests that some of the Norwegian *Hostinella* is *Psilophyton* and possibly *P. goldschmidtii*. A careful search at Röragen is essential for the discovery of a specimen of *P. goldschmidtii* with both sporangia and anatomy.

The *Aphyllopteris* described by Halle looks to us much like lateral branch systems of *Psilophyton* from the Gaspé now that branching patterns in the genus are known to vary from dichotomous to pseudomonopodial to lateral. Without further detail, however, it is probably necessary to continue to refer them to *Aphyllopteris*.

The glabrous specimens for which Halle erected the name *Dawsonites arcuatus* are typical, in every respect, of the fertile lateral branches we describe for *P. dawsonii*. Lacking anatomy and attachment to main axis they must continue to be identified as *D. arcuatus* because they could be parts of *P. goldschmidtii* whose main axis is spiny whereas that of *P. dawsonii* is glabrous. However we have good evidence for the assertion that Halle's *Dawsonites arcuatus* is closely similar to the apical portion of a fertile branch system of *Psilophyton*. We borrowed several of his specimens including the one he illustrated (1916) as plate 3, figure 3. Uncovering of this specimen by Leclercq revealed the presence of an aborted branch in the axil of the first forking of the fertile branch system, (Pl. 17, fig. 4) and of many, not simply a few, sporangia borne in a large three-dimensional cluster just as they are borne in *Psilophyton*. *Dawsonites*, like *Psilophyton*, bore a three-dimensional, much dichotomized, fertile branch whose proximal forkings occasionally aborted and whose distal end was terminated by a large cluster of sporangia.

Ananiev and Stepanov (1969) described a *Dawsonites* from Western Siberia that fits both Halle's generic diagnosis and our interpretation of Halle's material. Successive dichotomies occur 90° round the stem from one another and some divisions look like trichotomies. The latter might be comparable to the "double dichotomies" that we found near the base of fertile lateral branches.

Halle's (1916) *Psilophyton princeps*, on the basis of epidermal structure and morphology of its spines, is *Sawdonia*.

Comments on characteristics of true *Psilophyton* as revealed by Lang and Croft and Lang from Scotland and Wales will be found in the Discussion.

## DISCUSSION

### *PSILOPHYTON*

It is now clear, over 110 years after the original description, why Dawson had so much trouble defining *Psilophyton* and why opinions on the most suitable specimen to use as holotype have varied. *Psilophyton* is both spiny (*P. princeps*) and glabrous (*P. dawsonii*). It may be found as compressions or as petrifactions and they differ in appearance. It consists of both fertile branches and vegetative branches which are usually preserved independently. Its branching is three-dimensional so that only portions of the plant appear on any one split surface. It occurs on the Gaspé Peninsula in or near strata containing other plants such as *Sawdonia, Crenaticaulis, Trimerophyton,* and *Taeniocrada* none of which was known, in present-day detail, to Dawson or to subsequent workers for many years.

An apparent confusion of three, probably four, plants is seen also in Lang (1932) where he reported *Psilophyton* from Upper Siegenian strata in Scotland. His figures 17-20, 22, 24, 33, 34, 36-70 on plates 2-4 illustrate *Sawdonia* whereas his figures 25-32 illustrate specimens which are, with present knowledge, best assigned to *Psilophyton goldschmidtii*. This action was alluded to by Lang. His figures 21, 23, 35 can not be assigned to either *Sawdonia* or *Psilophyton* and this is also the case with figures 72-77. In fact all of those fragments best would be considered as indeterminable vascular plant fossils or "kept apart as *Hostinella* sp." (Lang, 1932 p. 516). The paired sporangia illustrated in his figures 78-79 and the spores from the specimen in figure 79 that are illustrated in figures 80-82 are best kept with *Dawsonites arcuatus* as Lang suggested. The *sporae dispersae* in his figures 83-86 are of the same type as those obtained directly from the sporangia and, therefore, are easily kept together with *D. arcuatus*. Essentially, Lang maintained an excellent order among the plants he examined, particularly when one takes into account the state of knowledge of Devonian plants at the time, as well as the nomenclatural confusion associated with them. Croft and Lang (1942) faced the same problem with their identification of cf. *Psilophyton princeps* (figs. 8-15, pl. 9). The plant bore lateral sporangia and its stem was ornamented with small spinelike protuberances. This latter characteristic led them to associate the plant with *Psilophyton*, but the position of the sporangia caused them to doubt the wisdom of identifying the plant unequivocally with *Psilophyton princeps*. The plant is neither *Psilophyton* nor *Sawdonia* and should be restudied as it represents an ornamented form that belongs among the zosterophylls. Its sporangia are stalked and turned upward along the margins of the axis much as one sees in *Zosterophyllum* and *Rebuchia.* In their figures 16-19, plate 10 they illustrate specimens that may be fragments of *Psilophyton.* However, they wisely assigned them to *Dawsonites* and corroborated Halle's diagnosis of that genus in their description as they wrote: "Fertile region consists of a branch which subdivides repeatedly, the fine divisions bending in a way which suggests that the fusiform sporangia in which they end were pendant. The fertile branches arise laterally from broader axes and appear to have been radially arranged." All the features mentioned by Croft and Lang we have now confirmed in serial section and by uncovering three dimensional branch systems. Thus *Dawsonites* is similar to fertile branches of *Psilophyton dawsonii* but lacks main stems and vegetative branching.

*Psilophyton* has become at last a plant, not simply a fossil fragment. It was erect. Its main axis divided by equal dichotomy. It bore zones of vegetative lateral branches in an irregular spiral. Some of these branches forked dichotomously at varying intervals and finally terminated in slender blunt, sometimes recurved apices. Others were branched pseudomonopodially, bearing branchlets alternately and distichously. Some of the latter were elongate and some much shortened. The short branchlets even simulate precursors of leaves. In zones alternating with the vegetative branches fertile branching systems arose alternately and distichously. Branching of the fertile system was basically dichotomous. Usually six dichotomies, each at 90° around the axis from the preceding, resulted in a cluster of 64 terminal sporangia. However, the first two of these six dichotomies were unusual. Each was in reality two closely spaced dichotomies which would be expected to result in three axes. But one of the three axes aborted leaving two, thus simulating a single dichotomy. However, with care the stump of the aborted branch can be demonstrated. We have referred to this branching as a double dichotomy but count it as one when we say that the fertile system dichotomizes six times. Each sporangium has its own short stalk yet the sporangia always appear to be paired because intervals between dichotomies decrease steadily from base to apex of fertile branches. Sporangia are fusiform and dehisce longitudinally, a feature of many geologically younger vascular plants. Spores were smooth but characterized by curvaturae perfectae and by triangular darkened areas of the proximal surfaces along the commissures. Dawson suggested *Psilophyton* was rhizomatous and we have reason to believe him correct although his "rhizomes" have since proved to be stems of *Taeniocrada* and our evidence is not yet definitive enough to publish.

Anatomically *Psilophyton dawsonii* is remarkably well preserved. Its main axes were characterized by a massive, terete xylem strand ¼ the diameter of the stem. Its maturation was centrarch. It dichotomized in typical fashion. At the level of vegetative branching both its protoxylem and its metaxylem enlarged remarkably and traces to lateral branches, consisting of both proto- and metaxylem, branched from the central mass in an irregular spiral. The traces were of varying sizes. The larger usually supplied the more extensive vegetative laterals. Like the main axis they were centrarch. Traces in the lateral branches divided dichotomously in the smaller branches and forked alternately and distichously in some of the larger. They become successively smaller toward the apices of all branches. Thus both morphologically and anatomically *P. dawsonii* is an extensive branching system. Despite the underlying uniformity of this branching system we suggest that the evolution of a distinction between major branches, leaves, and a rootlike function was underway. Organs that suggest large branches are laterals 2 and 8 on Axis B and 1 and 6 on Axis A (Text-figs. 4, 13). Organs that suggest the origin of leaves are illustrated on Text-figure 4 as branchlets 1/3 and 1/1 on branch 1 of Axis A and by extrapolation 2/1 and 2/2 on Axis B. Smaller organs are illustrated on Text-figure 4 as branchlets (?) 3, 4, and 6 on Axis B. Their mode of emission differs from that of larger branches and the stele of the stem changes markedly in size and shape while they are arising. This behavior recalls the stele of *Botryopteris antiqua* Kidston in the region where it produces adventitious roots (Benson, 1911). The slender, flexuous organs 3, 4, and 6 could not be followed to their apices and that portion of the reconstruction, Text-figure 13, is conjecture. Still another explanation of branches 3, 4, and 6 is that they were aphlebiae.

Above the level of profuse vegetative branching the terete xylem strand of the main axis branched less often and supplied fertile branch systems. Its protoxylem first became elliptical, then a group of cells became free and ultimately was surrounded by its own metaxylem. Opposite this trace the same series of events resulted in a second, higher trace. Branches thus appeared on two sides of the axis only, an alternate, distichous arrangement. At the base of a fertile branch the branch trace was almost rectangular in outline. The constancy of this outline, observed more than a dozen times, gives us the assurance that we can predict which branches were fertile even when they are without preserved sporangia. The rectangular trace soon dichotomized twice producing three strands, one of which aborted. The two remaining strands each repeated the two closely spaced dichotomies and again one of the three strands aborted. Subsequent divisions were normal, simultaneous dichotomies each 90° round the stem from the preceding. Thirty two apices resulted and each bore two stalked sporangia. A strikingly large vascular strand continued up into the very base of each sporangium.

Histologically the xylem was surrounded by phloem in which we have failed to find evidence of sieve areas. Phloem cells are vertically elongate and parenchymatous. The inner cortex when preserved is parenchymatous. Outer cortex was composed of thick-walled elongate cells whose end walls were transverse or slightly oblique, hence collenchymatous rather than sclerenchymatous. Underneath stomates some of the thick-walled cells were replaced by parenchyma that either disintegrated when young or was rarely preserved. In either case substomatal chambers resulted. The epidermis was small-celled and interrupted only by guard cells of which we have few details.

The anatomical resemblance of sporangia to small branches is striking. Sporangia consisted of an epidermis with guard cells and a hypodermis like that of branches. Substomatal chambers were produced as in branches, and the innermost layers were of parenchyma. During maturation many of the wall cells broke down but a membrane, probably consisting of the inner tangential walls of the innermost parenchyma, remained. In compression specimens the sporangial wall was reduced to an outer carbonized layer (remnants of epidermis and some hypodermis) and a free membrane surrounding the spores. Lang found these same two layers on three occasions (1931, 1932, and with Croft, 1942) and Hopping (1956) described two identical layers in *Trimerophyton.* Dehiscence was longitudinal and in a pair of sporangia was along surfaces that faced one another. Empty sporangia still contained the membrane hence we believe that it normally was not lost at dehiscence. Only when sporangia are chemically macerated does the membrane come out. Clusters of spores are often found in the calcareous pebbles. The clusters are the size of the inner sporangial membrane giving rise to the suggestion that they may have come out of sporangia as a mass rather than individually. Alternatively these masses may have been released by the decay of sporangial walls.

The xylem cells were annular, spiral, and scalariform. Typically however the secondary wall formed more than just scalariform bars. It was deposited in various patterns between them as well. The result was a row or rows of circular areas between the bars or, occasionally, vertical connections between the bars. The circular areas seem to us to be homologous to pits.

## CLASSIFICATION

The new understanding of the plants called *Psilophyton* necessitates a reevaluation of their taxonomic position. *Psilophyton* is still essentially a leafless plant bearing terminal sporangia, the classical definition of Psilophytales, placed by Eames (1936) in the subdivision Psilopsida. Yet *Psilophyton* is a much more complex plant than *Cooksonia* or *Rhynia* both of which conform to the classical definition. Some examples of this increased complexity are the segregation of vegetative and fertile portions of the plant, the tendency toward pseudomonopodial branching that results in lateral branches, the differentiation of smaller (more leaf-like) from larger lateral branches, the restriction of sporangia to lateral instead of main axes, the profuse branching of the fertile branch system and the resulting mass of sporangia, the massive size of the xylem strand compared to the slender strand of *Rhynia,* the complex branching pattern of this strand in various parts of the plant, the more complex secondary wall structure of tracheids in *Psilophyton.* In other words *Psilophyton* can no longer be retained in a group designed for simple plants like *Rhynia.* Its closest relatives appear to be *Trimerophyton robustius* (Dawson), Hopping, 1956, and *Pertica quadrifaria* Kasper and Andrews, 1972. *Trimerophyton* consists of a pseudomonopodially branched axis that bears laterals in three vertical rows. The laterals branch quickly into three each of which again branches into three branchlets. The latter dichotomize and then terminate in clusters of erect sporangia whose mature walls, like those of *Psilophyton,* consist of an outer carbonized layer and an inner, thin membrane around the spores. Only fertile branches have been found but their tendency to fork into three parts recalls the two double dichotomies that we find in fertile branches of *Psilophyton.* Apparently, however, there was no abortion in *Trimerophyton.* The two genera are clearly distinct but equally clearly are closely related. Anatomy is unknown for *Trimerophyton.*

*Pertica* is also pseudomonopodially branched. Its laterals are borne spirally in four rows and show a tendency to be arranged in clusters of four (Kasper and Andrews, 1972, fig. 8). All laterals branch dichotomously. Each dichotomy is at right angles to the next. Sterile branches terminate in slender tips. Separate fertile branches terminate either in slender tips or globose masses of sporangia that radiate in all directions. *Pertica,* like *Trimerophyton,* was found only as compressions so that anatomy and histological details are unknown.

It has been recognized for some years that Psilophytales had become a meaningless category as one after another Devonian plant was placed in the order without due consideration of the variability found or on the basis of too restricted evidence. Leclercq (1954), for example, pointed out the existence of two discrete evolutionary lines among psilophytes, those with terminal and those with lateral sporangia. Hueber (1964b) expanded this suggestion by describing the longitudinal *vs.* distal dehiscence in the two groups. Banks (1968b) took the additional step of naming three subdivisions of vascular plants to replace the one subdivision Psilopsida (Table 3). For *Rhynia* and allied plants he suggested Rhyniophytina, plants with terminal sporangia, longitudinal dehiscence and centrarch maturation. Zosterophyllophytina included *Zosterophyllum* and allied genera with lateral sporangia, distal dehiscence and exarch maturation. For reasons given above, he added a third subdivision, Trimerophytina, for plants more complex than *Rhynia* but still with terminal sporangia (in large masses) and longitudinal dehiscence. *Psilophyton,* the only genus for which anatomy is known, has a large centrarch xylem strand. Elimination of Psilophytales was long overdue but these three new subdivisions are only a beginning of the classificatory changes that are required by plants in the Devonian flora. A picture of the many genera for which ultimately other subdivisions must be established can be obtained by studying the excellent account by Høeg (1967), *in* Boureau. The major hindrance to further categorizing is the paucity of data for the fossils in question. The same drawback is seen in Rhyniophytina. Only *Rhynia, Horneophyton,* and *Cooksonia* are really well characterized. The other genera listed lack many essential details and may ultimately have to be moved elsewhere.

Table 3. Classification. Three subdivisions of vascular plants (their characteristics given in text) designed to replace in part the now obsolete category Psilopsida. For other, as yet not reclassified, "psilophytes" see Høeg (1967). Some of the genera of Rhyniophytina may have to be transferred elsewhere when understood fully, *e.g. Hedeia, Yarravia.*

Division Tracheophyta

Subdivision — Trimerophytina Banks, 1968b
  *Psilophyton* Dawson, 1859
  *Trimerophyton* Hopping, 1956
  *Pertica* Kasper and Andrews, 1972
  *Dawsonites* Halle, 1916
  *Hostinella* Stur, 1882 (in part, cf. Banks, 1968a)

Subdivision —

Rhyniophytina Banks, 1968b
  *Rhynia* Kidston and Lang, 1917
  *Horneophyton* Barghoorn and Darrah, 1938
  *Cooksonia* Lang, 1937
  *Steganotheca* Edwards, 1970b
  *Taeniocrada* D. White, 1902
  *Hicklingia* Kidston and Lang, 1923
  *Eogaspesiea* Daber, 1960
  *Hedeia* Cookson, 1935
  *Yarravia* Lang and Cookson, 1935

Subdivision —

Zosterophyllophytina Banks, 1968b
  *Zosterophyllum* Penhallow, 1892
  *Gosslingia* Heard, 1927
  *Crenaticaulis* Banks and Davis, 1969
  *Sawdonia* Hueber, 1971
    (syn. *Psilophyton princeps* var. *ornatum* Dawson)
  *Rebuchia* Hueber, 1970 (syn. *Bucheria* Dorf)
  *Bathurstia* Hueber, 1972

## STRATIGRAPHIC OCCURRENCE

The oldest plants proved to be vascular are *Cooksonia* Lang (1937) and *Steganotheca* Edwards (1970b). Both are found at the base of the Pridolian (Downtonian) (Banks, 1972), the youngest stage of Silurian. Both are naked, dichotomizing plants that bore terminal sporangia. Their basal parts are still unknown. Both are typical members of Rhyniophytina. The oldest Zosterophyllophytina appear to be Gedinnian (Banks, 1972). These two groups appear to be the only typical, proven vascular plants until about mid-Siegenian time when several additional groups appeared, as if a burst of evolution had occurred. One example of a new type is the genus *Krithodeophyton* Edwards (1968). It combines characteristics of two groups and perhaps belongs in the barinophytes. A second example is the lycopods which appeared for the first time in Siegenian and a third is a *Psilophyton*-like plant represented by fragments referable to *Dawsonites arcuatus* Halle which appeared in late Siegenian time in Wales (Croft and Lang, 1942).

*Psilophyton* in Norway, on the Gaspé Peninsula, in the State of Maine, and in Siberia is found in continental strata whose precise age is difficult to assess. It may be late Emsian or early Eifelian. In either case these more abundant collections are at most only a few million years younger than the earliest occurrence in the Siegenian of Scotland (Table 1) and it would be accurate to state that abundant *Psilophyton* occurs close to the Emsian-Eifelian (Lower-Middle Devonian) boundary. Presumably it persisted into later Middle Devonian but critical specimens and trustworthy evidence of the plant are sparse except in Stockmans (1940). We know no valid evidence of Upper Devonian *Psilophyton.* Carefully studied specimens reported as *P. princeps* such as those of Hueber and Grierson (1961) from the Upper Devonian of New York State are now referable to *Sawdonia ornata* (Dn.), Hueber and not to *Psilophyton.* All other records of late Devonian *Psilophyton* need equally careful analysis.

## PHYLOGENETIC CONSIDERATIONS

Trimerophytina, represented by one genus (*Psilophyton*) whose morphology and anatomy are now well characterized and by two genera (*Trimerophyton* and *Pertica*) known only by their external morphology, demonstrate the evolutionary potential to continue the adaptive radiation of vascular plants on land that started with a burst in mid-Siegenian. Given the time-tested morphological dicta - overtopping, planation, webbing, recurving, reduction, and increased complexity - the trimerophytes represent a natural plexus at an evolutionary level whence such groups as coenopterids and progymnosperms might evolve as the flora of Eifelian and Givetian diversified.

The trimerophytes can only be regarded as an elaboration of the rhyniophyte level of evolution resulting from the interplay of overtopping and elaboration in both anatomy and morphology. Some of the still primitive characters of trimerophytes are the axis-like sporangial walls with many layers of differentiated cells and with stomata on their surface and vascular tissue continuing into the base of sporangia, three dimensional (non-planated) branching systems, retention of some dichotomous branching, and a solid protostele.

Certain characteristics of trimerophytes that are retained by, or modified in, younger groups are worthy of mention. Terminal, fusiform sporangia that dehisce longitudinally were abundant in Devonian strata once they appeared in trimerophytes. Banks (1970) illustrated this on his figures 5-9. The differences between the many genera (*e.g. Rachophyton, Pseudosporochnus, Calamophyton, Tetraxylopteris,* and *Archaeopteris*) in which they are found can all be accounted for by well-understood morphological changes and the similarities between them are sufficiently marked to suggest an elaboration on the evolutionary level represented by the trimerophytes.

Variability of branching patterns in trimerophytes provides a starting point for subsequent evolutionary modification. On the basis of our present knowledge, the main axis in all three genera branches pseudomonopodially and their laterals branch dichotomously, at least in part. Dichotomy is also known in the main axis of *Psilophyton*. The first two divisions of laterals in fertile branches of *Trimerophyton* produce three branchlets and the first two in *Psilophyton* result in strange abortions. Sterile lateral branches in *Psilophyton* are borne in a tight, irregular spiral whereas its fertile branches are loosely spaced and borne alternately and distichously. Laterals of *Trimerophyton* are borne tristichously, those of *Pertica* tetrastichously. Laterals of both *Psilophyton* and *Trimerophyton* are borne at an acute angle and are elongate whereas those of *Pertica* are almost horizontal and obviously compact. Laterals of *Pertica* tend to occur in groups of four along the stem. Ultimate branchlets of both *Psilophyton* and *Pertica* are slender, often recurved, and are three-dimensional structures. *Psilophyton* bears laterals of two kinds, as mentioned earlier, some of which may simulate precursors of leaves, others which seem to be precursors of major branches rather than lesser appendages. The smaller appendages of *Psilophyton* and the sterile branches of *Pertica* both simulate the dichotomizing, three-dimensional ultimate appendages of some aneurophytes which are planated in other aneurophytes. Trimerophytes, it seems, were well provided with evolutionary potential if leaves evolved from branch systems as is usually hypothesized.

*Psilophyton* is the only trimerophyte whose anatomy is known. Both *P. princeps* and *P. dawsonii* are protostelic, the stelar type long held to be primitive. Current evidence indicates that it was the first type to appear in the fossil record. Equally acceptable is the hypothesis (Bower, 1930) that variously lobed steles evolved next, followed by dissected steles. The stele of *Psilophyton* is much enlarged over, and more complex than, that of the rhynia-type. Even the tracheids of *Psilophyton* can be interpreted as characteristic of a plexus whence evolution could have proceeded in several directions. The deposition of secondary wall in various patterns between the scalariform bars is seen as a stage in the evolution of circular bordered pits. Evolutionary derivatives of *Psilophyton* can be expected to have sharply defined circular bordered pits, as for example in the progymnosperms, or may retain only the scalariform type of pitting such as characterizes many ferns.

Some specific groups whose origin can be traced to ancestral forms represented by *Psilophyton*-like organisms are worthy of comment.

The evolutionary origin of coenopterid ferns has been uncertain although some workers have postulated that a dichotomizing "psilophyte" might serve as a prototype of a coenopterid such as *Botryopteris* whose stem stele and foliar bundle are little different in size. Morgan and Delevoryas (1954) suggested that the protostelic coenopterids *Botryopteris, Apotropteris, Anachoropteris* and *Tubicaulis* represented steps in specialization of petiolar traces from an original dichotomous branching system. *Psilophyton* can be regarded as an early step in such a series. It branches dichotomously and it also branches unequally. The rectangular strand at the base of its fertile branch could be regarded as an earlier step than either ad- or abaxially curved petiolar strands of coenopterids. Either of the curved strands could have lost some metaxylem, leaving protoxylem in a peripheral position. Bulges on the stem xylem often precede the departure of petiolar traces in coenopterids. Similar bulges are found at the base of fertile branches of *Psilophyton* (Pl. 20, fig. 32), and even more markedly at the base of its extensive vegetative branching (Pl. 24, figs. 63-65). In the latter position one even finds radially aligned metaxylem as in *Zygopteris* (*e.g.* Baxter, 1952). The scalariform, multiseriate scalariform (*e.g.* Delevoryas and Morgan, 1952) and circular pitted tracheids found in coenopterids can be derived from the scalariform and interconnected scalariform tracheids of *Psilophyton.*

Coenopterid ferns bear endogenously produced, diarch roots often in areas where both the number of protoxylem strands and the amount of primary xylem in the stem have increased noticeably (Benson, 1911). This anatomical change, also found in our vegetative Axis B in the region of profuse branching (Pl. 24, fig. 62-65) prompted our speculation that appendages 3, 4 and 6 (Text-fig. 4) might be precursors of rootlike organs rather than precursors of leaves as we have treated them earlier. At present this can be no more than speculation because appendages 3, 4, and 6 are neither exarch in maturation of xylem nor are they endogenous in origin. Yet it would hardly be expected to find such differentiated structure in a plant from the late Lower Devonian that is in the early stages of evolution. Coenopterids also often bear organs referred to as aphlebiae (Holden, 1930; Baxter, 1951, 1952) which have been variously called rootlets, secondary leaf pinnae, a delicate protective tissue, scale leaves and even reduced pinnules. Our appendages 3 and 4 may equally well represent precursors of these exogenously produced organs.

An extremely simple coenopterid such as *Rhabdoxylon* (Dennis, 1968; Holden, 1960) is little different from *Psilophyton* in its terete, protostelic, centrarch stem stele, and its unequal dichotomies that produce circular to ovoid petiolar strands with a single adaxial protoxylem group.

*Psilophyton* could even be thought to foreshadow the axillary branches found in some coenopterids if one accepted Baxter's (1951) suggestion that the leaf subtending an axillary branch "migrated" down the branch from an originally more distal position. In the vegetative system of *Psilophyton* some appendages on branches may be precursors of leaves which could undergo the phylogenetic "move" visualized by Baxter (*e.g.* branchlet 1/1 on branch 1 of axis A in Text-fig. 4). *Psilophyton,* in other words, displays several of the characteristics that one might envisage in a plant that was still "plastic" and at an evolutionary level somewhat below the coenopterids.

Delevoryas (1962, pp. 79, 80) outlined some of the reasons for not considering coenopterids to be ancestral to ferns. However, trimerophytes were less advanced than coenopterids and not subject to the same difficulties. They were more "plastic" and, it seems to us, could still have evolved in the direction of ferns as well as of coenopterids, but so far we can point to no Devonian ferns with which to test this hypothesis.

Progymnosperms were the other major group of Devonian plants whose origin might stem from plants at the trimerophyte level of evolution. The primary xylem of aneurophytes, the more primitive progymnosperms, was usually a lobed protostele with several protoxylem strands and with varying amounts of parenchyma (Scheckler and Banks, 1971a, b). The latter became more abundant both ontogenetically as in *Tetraxylopteris* and phylogenetically as in *Archaeopteris* until a mixed pith or a true pith was present. Thus the primary xylem of progymnosperms was somewhat advanced over that at the trimerophyte level. But the evolution of a cambium and secondary xylem, probably about Eifelian time, was the more striking advance found among progymnosperms. The resulting secondary tissues were markedly gymnospermous in character. Morphologically, progymnosperms were an elaborate branching system, more elaborate than trimerophytes but marked by the same main axis and three-dimensional lateral branch systems that bore smaller ultimate appendages that were sometimes three dimensional, sometimes planated. It is difficult to think of this system as more than an elaboration of the branching systems of trimerophytes. Certain lateral branches of aneurophytes were fertile. They dichotomized. They branched pinnately. They bore sporangia terminally and the whole system consisted of masses of sporangia. But again the planation of a fertile branch of a trimerophyte and the webbing of some of its members could easily result in the fertile system of an aneurophyte such as *Tetraxylopteris* or *Protopteridium* (Bonamo and Banks, 1967; Leclercq and Bonamo, 1971).

## SUMMARY

A new species, *Psilophyton dawsonii,* sp. nov., is proposed for specimens comprising petrifactions and compressions from two localities in late Emsian-early Eifelian (late Lower-early Middle Devonian) sediments in Gaspé, Quebec, and northern Ontario, Canada. The plant at all levels of branching is circular in cross section. As yet, the apex and base of the plant are not known. Maturation of the xylem is centrarch, there is no secondary growth and the strand is circular in cross section in all parts except in the base and

lower branching levels of fertile branches. The protoxylem consists of narrow spiral and scalariform elements. The surrounding metaxylem tracheids have broad scalariform bordered pits in which additional secondary wall material has outlined one to three, most commonly one or two, horizontal rows of circular, pitlike areas. The number of pitlike areas in a row varies with the width of the tracheid. The phloem, rarely preserved, is centrifugal to the xylem strand and is composed of elongate cells with slightly oblique end walls in which no sieve areas have been observed. An inner cortex, which probably functioned as assimilating tissue, immediately surrounds the stele and consists of narrow, thin-walled, loosely arranged parenchyma cells. This tissue is followed by an outer cortex of thick-walled, collenchymatous cells which form a hypodermal layer that is continuous around the axis except at points where substomatal chambers have developed. There, directly beneath the stomata, the thick-walled cells are replaced by parenchyma which subsequently disintegrates and a substomatal chamber results. Epidermis is rarely recognizable but where it can be defined the cells are small and tangentially rectangular in cross section and vertically elongate in longitudinal section.

Branching of the main axis is into two equal parts, the xylem strand in both is terete. Fertile lateral branch systems are easily recognized in cross section by their distinctive xylem strand which is rectangular in outline. The first two divisions of the strand are closely spaced dichotomies, usually characterized by the abortion of one of the three resulting branches. Each of the remaining two branches, after elongation, again undergoes two close dichotomies in which one of the three resulting branches aborts. We refer to these branchings followed by abortion as "double dichotomies." Subsequent branching is strictly dichotomous and the distance between dichotomies decreases distally. A strand of xylem extends up to the sporogenous tissue of each of the sporangia which terminate the ultimate divisions. The sporangia form loose clusters consisting of 32 pairs with members of each pair arranged such that their lines of dehiscence are on facing surfaces. The number of sporangia in the clusters may be less as a result of abortion of a sporangium or suppression of a dichotomy. The number may be increased by the addition of a dichotomy in the system. Throughout the lateral branch systems the dichotomies occur 90° around the stem from one another, producing three dimensional structures. The fertile branches are produced from the main axis in alternate and distichous arrangement in zones which alternate with vegetative branch systems. The traces to, and xylem strand of, vegetative branches are circular in cross section. The traces are produced spirally in relatively large numbers within an extremely short vertical distance. The plant is leafless but some of the vegetative branchlets with terete, delicate, recurved or straight, ultimate tips could be interpreted as precursors of leaves.

Spores isolated from the sporangia are 40-75$\mu$ in diameter. Their exines are smooth. Curvaturae are present and they usually follow the equatorial margin of the spores. Commissures are outlined by darkened areas that may be straight or curved. The spores most closely resemble the spore genus *Retusotriletes.*

The fertile systems of *Psilophyton* are like those described by Halle, and for which he proposed the name *Dawsonites.* We maintain *Dawsonites* as a form genus when only a portion of the fertile system is found and can not be shown by technique to be *Psilophyton.*

*Psilophyton dawsonii* may be distinguished from *P. princeps, P. kräuselii, P. arcticum, P. rectissimum,* and *P. goldschmidtii* by its lack of spines or hairs which characterize the other species. The sporangia of *P. dawsonii* are smaller than those of *P. princeps* and larger than those of *P. kräuselii.* The glabrous species *P. forbesii,* for which sporangia are perhaps known, is not certainly enough described with regard to the arrangement and branching of its fertile shoots and the number of sporangia they bear to make meaningful comparisons with *P. dawsonii.*

The stratigraphic range of species of *Psilophyton* can not be clearly defined. The oldest *Psilophyton*-like fragments, referable however to *Dawsonites arcuatus,* are of late Siegenian age while the youngest well documented specimens are of Eifelian age. The plexus of *Psilophyton* spp. had its acme during Emsian-Eifelian time.

Phylogenetically *Psilophyton* and the other genera in the subdivision Trimerophytina (*i.e., Trimerophyton* and *Pertica*) demonstrate the evolutionary potential to continue the adaptive radiation of vascular land plants and serve as the source whence coenopterids and progymnosperms evolved.

## ADDENDUM

Shortly after our paper was in press another, also in press, containing descriptions of two new species of *Psilophyton* came to our attention. The new species are *P. microspinosum* and *P. dapsile* Kasper, Andrews, and Forbes in "New fertile species of *Psilophyton* from the Devonian of Maine", American Journal of Botany, 1974. *P. dawsonii* is readily differentiated from *P. microspinosum* in that its axes are not spinous and that its sporangia are pendulous rather than standing erect. Sporangia of *P. dawsonii* are larger than those of *P. dapsile*, 3.0-5.0 mm × 1.0-1.5 mm *vs.* 1.7-2.1 × 0.5-0.9 mm and are less abundant, approximately 32 pairs as opposed to possibly 256 pairs if the reported estimate of 256 pairs is substantiated. No anatomical detail is known for the species described by Kasper, *et al.*, and thus comparison with *P. dawsonii* is precluded.

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# PLATES

## EXPLANATION OF PLATE 17

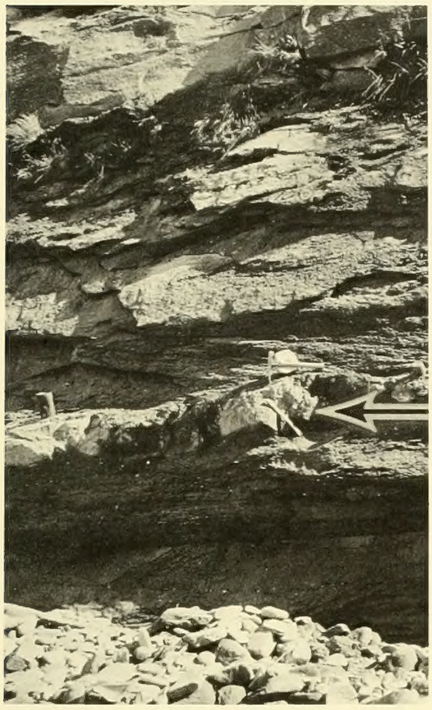
*Figure* *Page*

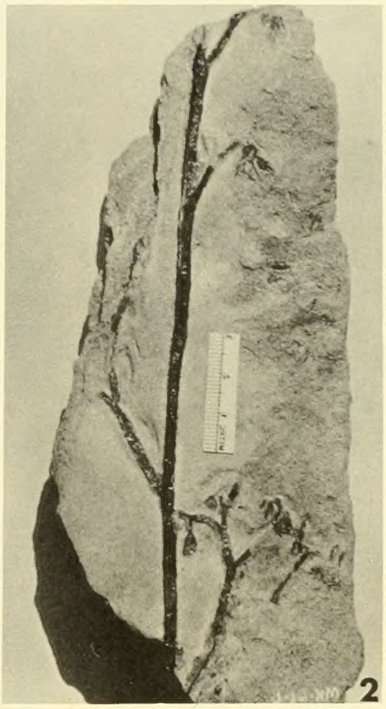
1-3, 5-10. *Psilophyton dawsonii*, sp. nov. ........ 105

4. *Psilophyton goldschmidtii* Halle ........ 107

1, 5, 6. *P. dawsonii* from Gaspé; 2, 3, 7-10. From Abitibi River, Ontario; 4. *P. goldschmidtii* Halle from Röragen, Norway.

1. Boulder (arrow) containing *P. dawsonii* in place in cliff east of Douglastown, P. Q. on Gaspé Peninsula; × 1/40.
2. Specimen from Abitibi River locality prior to uncovering by needles (GSC 32719); × 1/2.
3. *P. dawsonii*, sp. nov. ........ 105
   Final stage in uncovering, by F. M. Hueber with steel needles, of a fertile branching system that terminates in 64 sporangia. Specimen from Abitibi River (GSC 32720); × 2/3.
4. *P. goldschmidtii* Halle ........ 107
   Borrowed from the Halle Collection Swedish Museum of Natural History and uncovered by Leclercq to show an aborted branch (arrow) at first "double dichotomy" of fertile branch system; × 1.
5. Tips of sterile (vegetative) branch system macerated out of cobble and embedded in bioplastic. Three dichotomies are seen here to be at right angles to one another. Branch system was thus three-dimensional (CUPC 192); × 5.5.
6. Final dichotomy of vegetative branch system, also in bioplastic. Note that tips are tapering and rounded, not spinelike (CUPC 192); × 13.
7. One tracheid from pyritized axis at Abitibi River to show its identity to those from Douglastown; cf. Figures 23, 25, 26 (GSC 32720a); × 400.
8. Transverse section of xylem strand from pyritized axis (Abitibi River) showing division of protoxylem below attachment of a fertile branching system (GSC 32720b); × 70.
9. Same axis as Figure 8 higher up showing trace to fertile branch (GSC 32720c); × 70.
10. Same axis as Figures 8 and 9 showing xylem of main axis (below) and rectangular strand to fertile branch (above). Compare this series from Abitibi River with the series (Figs. 31-34) from Douglastown (GSC 32720d); × 30.

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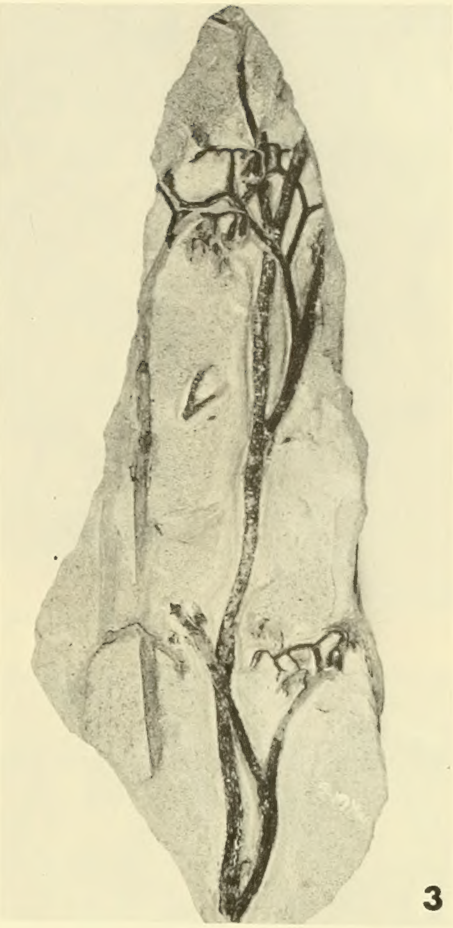
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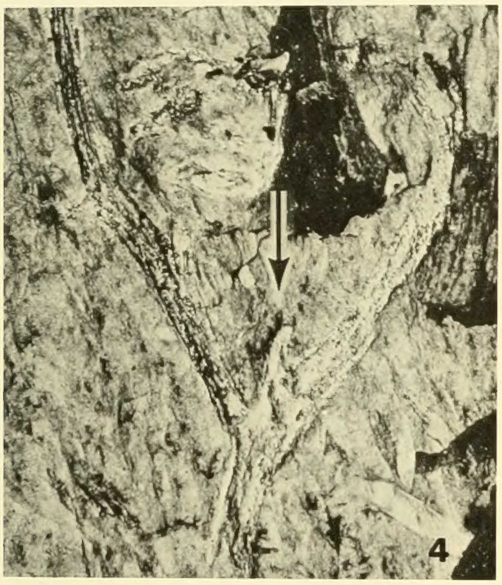
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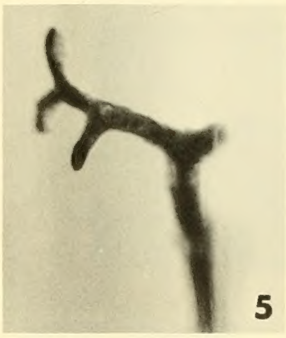
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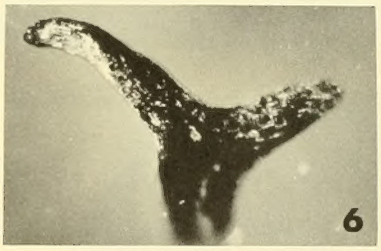
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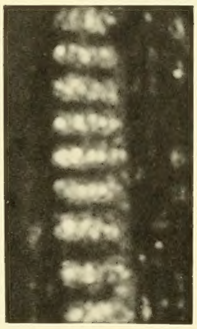
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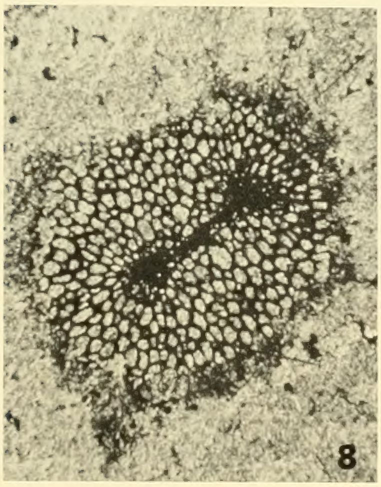
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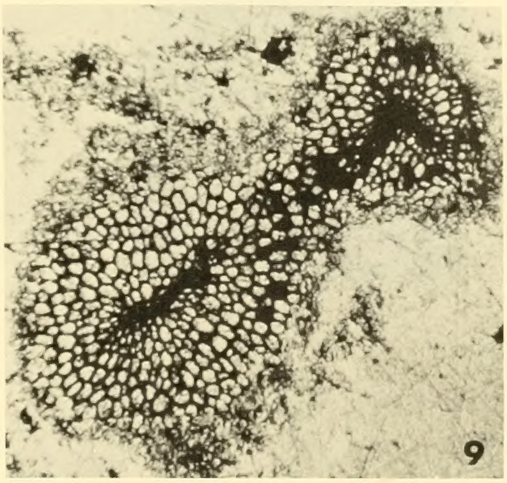
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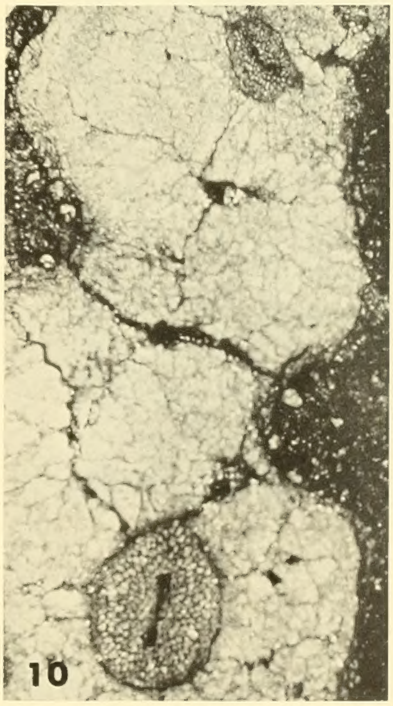
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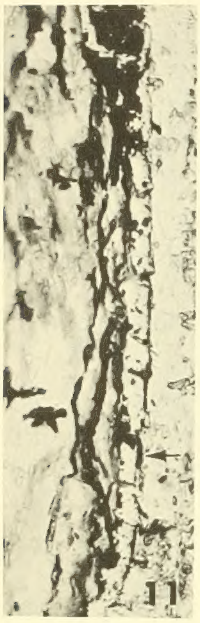
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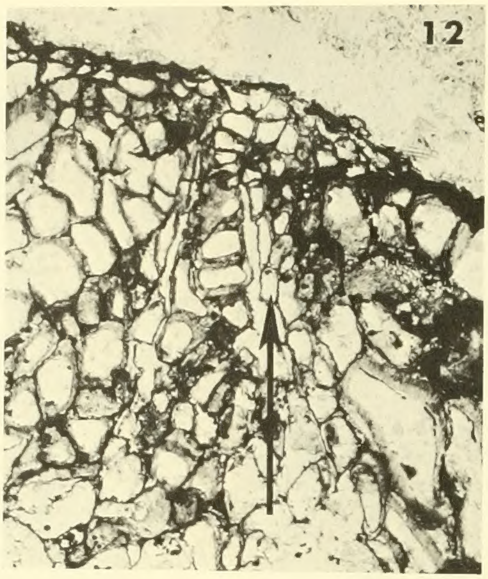
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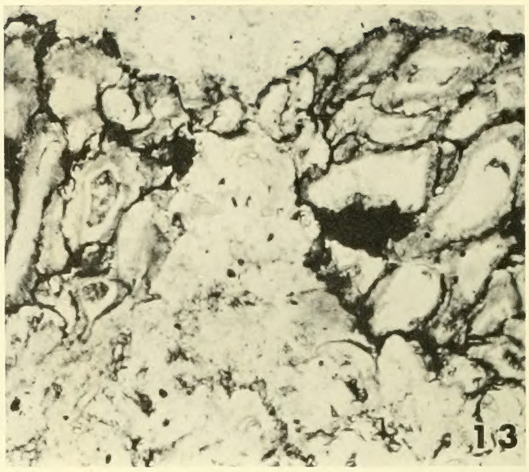
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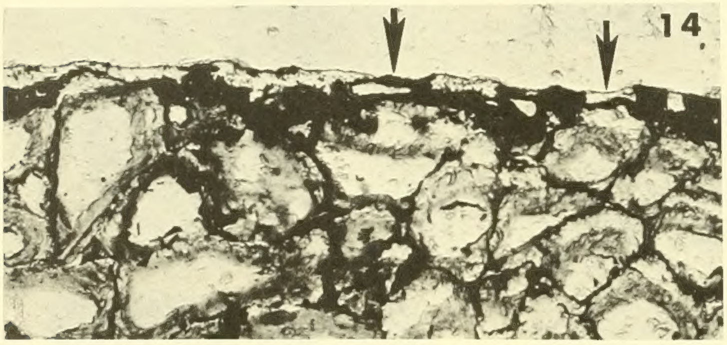
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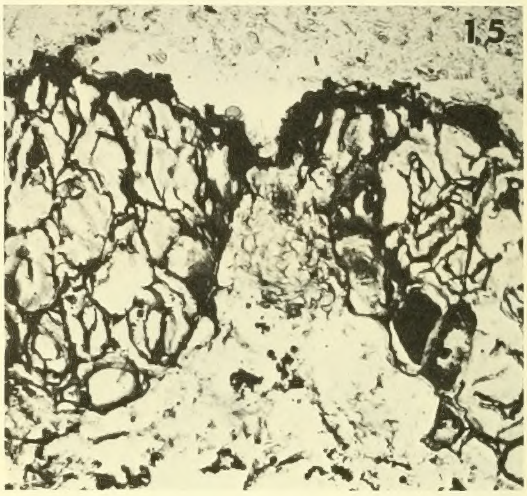
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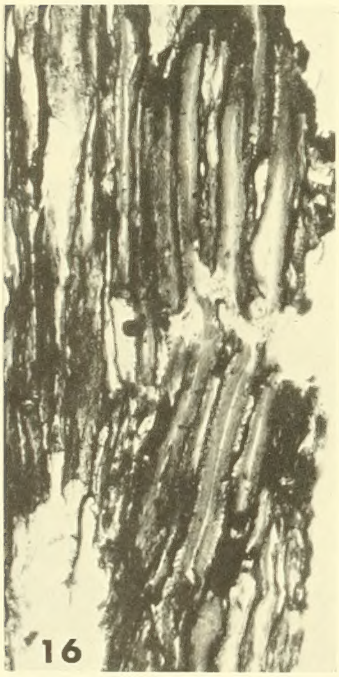
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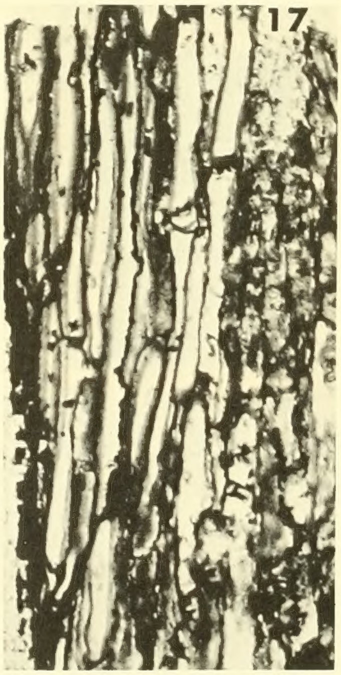
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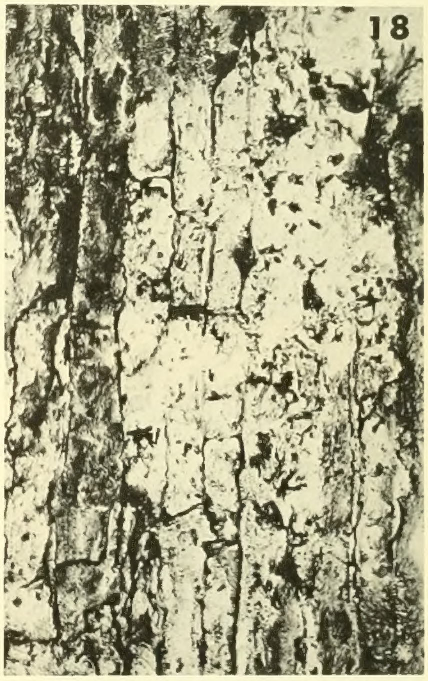
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## EXPLANATION OF PLATE 18

*Figure* *Page*

11-18. *Psilophyton dawsonii,* sp. nov. .................................................. 105

Histology.

11. Epidermis (arrow) in longitudinal section (CUPC 191 — slide 35.1.bY.4). × 180.
12. One substomatal chamber still filled with intact cells, some parenchymatous (arrow), some collenchymatous (CUPC 192 — side 4.3.2Y.31); × 110.
13. Substomatal chamber below a pair of presumed guard cells (CUPC 192 — slide 4.4.1.3); × 140.
14. Epidermis (arrows) in transverse section (CUPC 192 — slide 4.3.2Y.35); × 145.
15. One substomatal chamber in which cells are disrupted and represented by debris (CUPC 198 — slide 34.3.1.13a); × 145.
16. Demineralized axis embedded in paraffin and microtomed. Several thick-walled collenchymatous cells well preserved (CUPC 194 — slide J1); × 100.
17. Collenchymatous (hypodermal) cells of outer cortex in longitudinal section, end walls transverse to slightly oblique (CUPC 191 — slide 35.1.1.17); × 105.
18. Inner cortex, parenchymatous cells in longitudinal section (CUPC 191 — slide 35.1.bY.4); × 140.

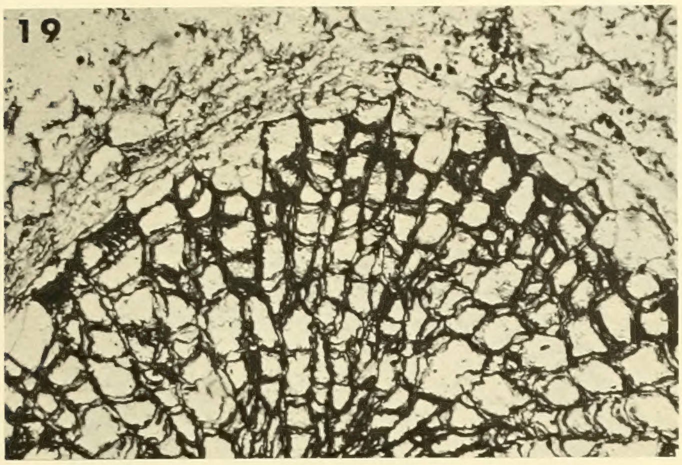
## EXPLANATION OF PLATE 19

*Figure* *Page*

19-28. *Psilophyton dawsonii,* sp. nov. .................... 105

Histology.

19. Phloem cells adjacent to xylem in transverse section (CUPC 192 — slide 4.3.2Y.35); × 110.
20. Phloem cells in longitudinal section (CUPC 192 — side 4.3.L.7); × 280.
21. General view of xylem in longitudinal section (CUPC 195 — slide 21.3); × 150.
22. Spiral element in protoxylem, longitudinal (CUPC 192 — slide 4.3.L.8); × 450.
23. Metaxylem tracheid showing scalariform secondary thickenings and interconnections between them that outline pitlike areas (CUPC 197 — slide 32.3bL.18); × 360.
24. Scalariform pitted tracheid derived from a demineralized axis that was embedded in paraffin and microtomed. Note resemblance of this cell to that in Fig. 23 (CUPC 194 — slide F2); × 715.
25. Scalariform-pitted tracheid with interconnections between the bars simulating the Williamson's striations characteristic of some lepidodendrids (CUPC 192 — slide 4.3.L.7); × 450.
26. Scalariform-pitted tracheid showing two rows of pitlike areas between the bars (CUPC 192 — slide 4.3.L.4); × 610.
27. Sectional view of scalariform bordered pits, longitudinal section (CUPC 191 — slide 35.1.bY.15); × 770.
28. Sectional view of scalariform bordered pits, enlarged (CUPC 191 — slide 35.1.bY.15); × 1205.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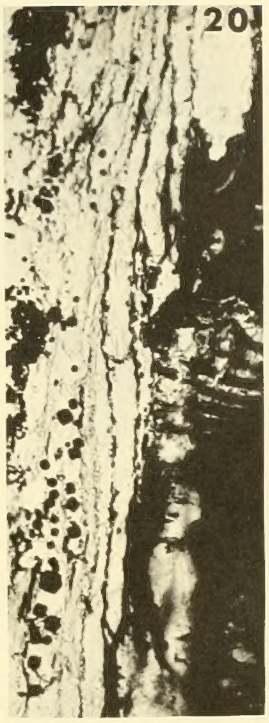
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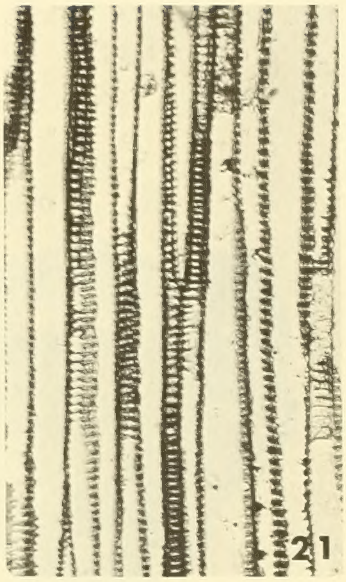
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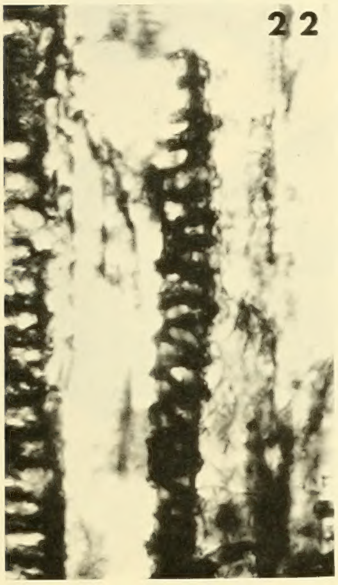
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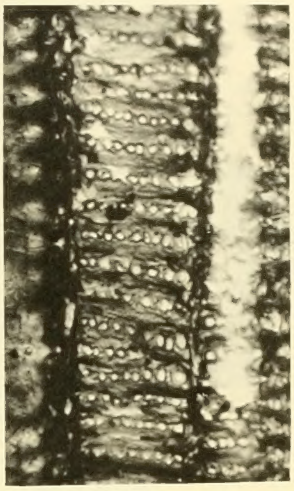
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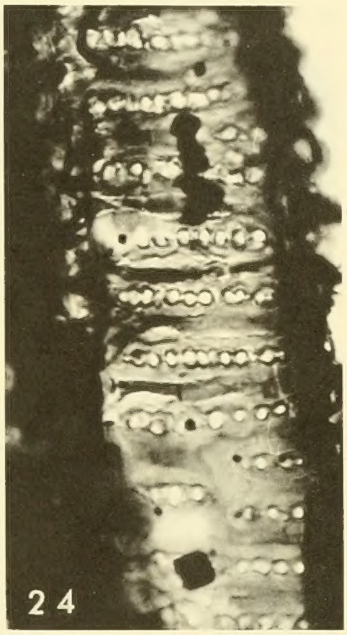
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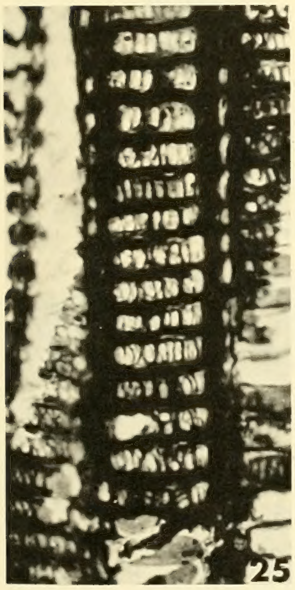
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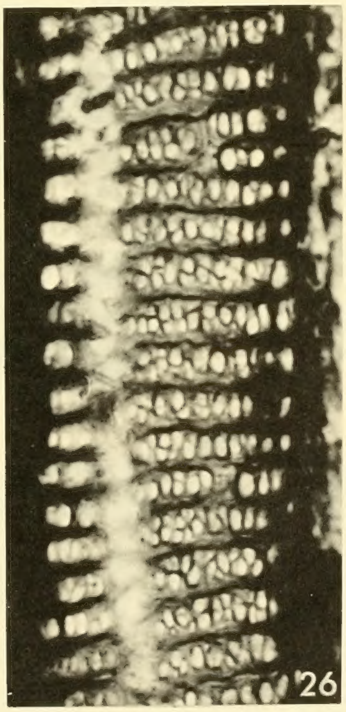
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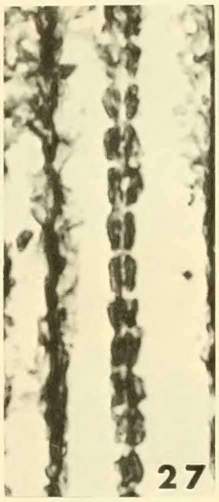
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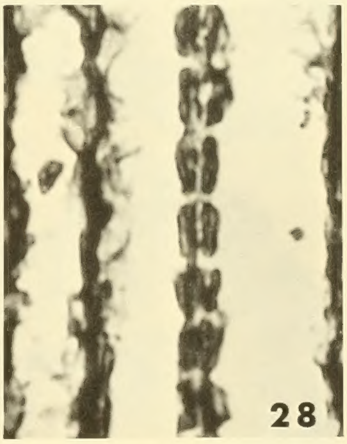
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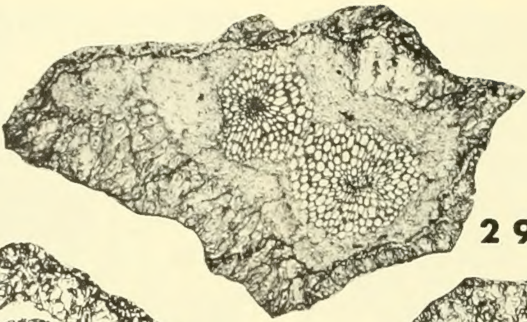
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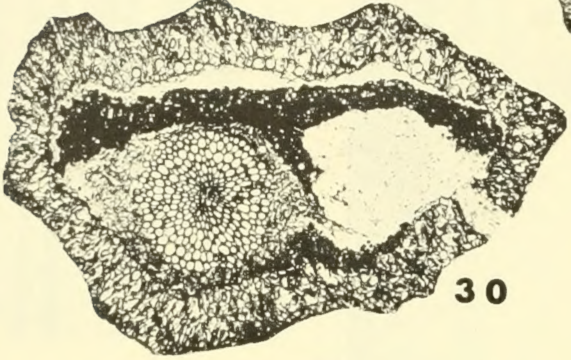
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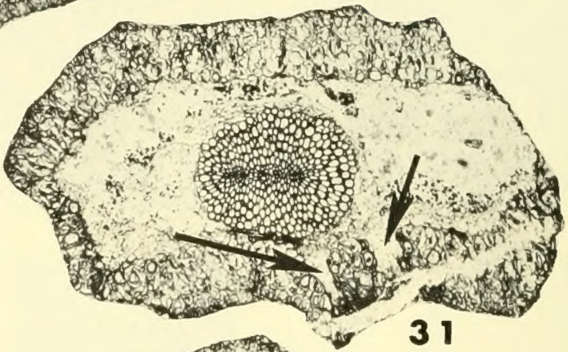
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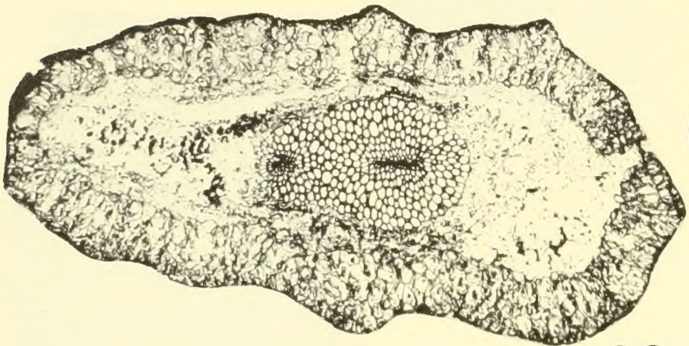
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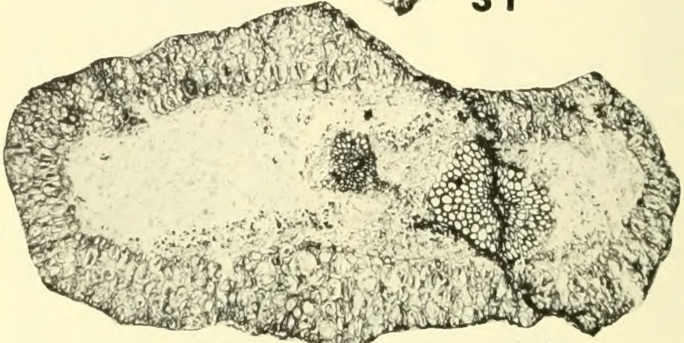
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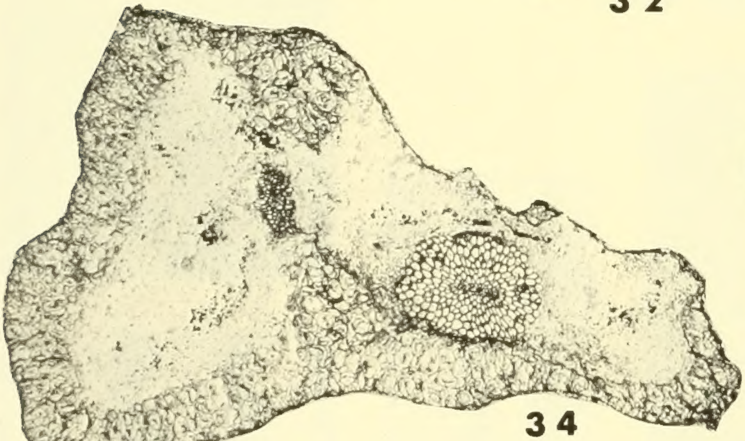
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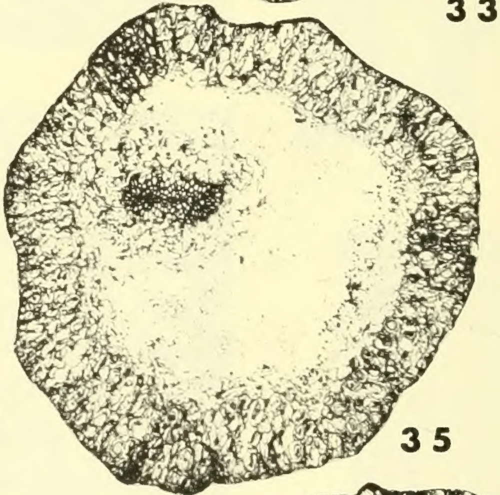
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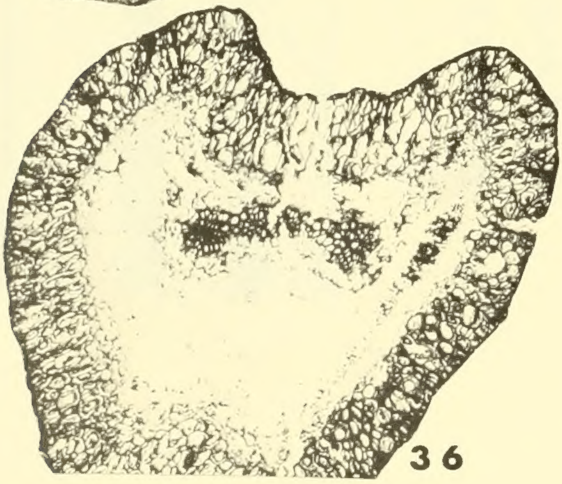
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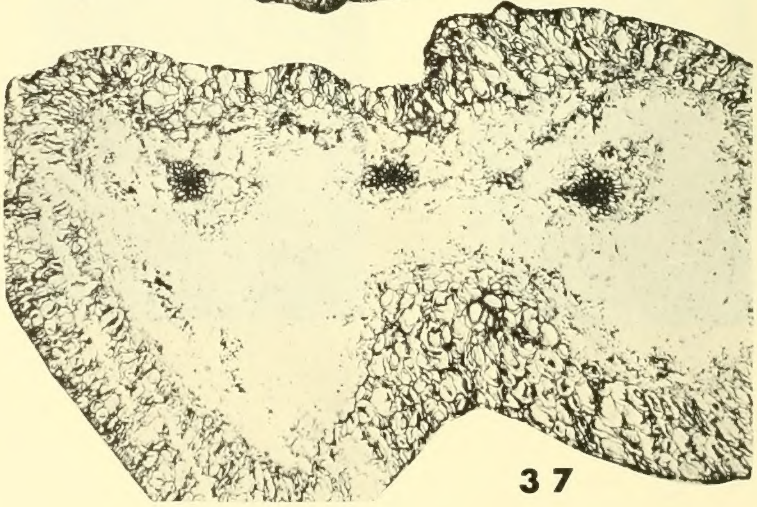
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## EXPLANATION OF PLATE 20

*Figure* *Page*

29-37. *Psilophyton dawsonii*, sp. nov. .............................. 105

Series of sections of main axis and fertile branch system arranged from base toward apex.

29. Dichotomy in a main axis below a fertile branch. Each new xylem strand has one centrarch protoxylem strand (CUPC 194 — slide 13.23); × 30.
30. Transverse section of main axis with one protoxylem strand at a higher level but still below origin of fertile lateral branch (CUPC 190 — slide 31.3.1.23); × 30.
31. Main axis now with two protoxylem strands and xylem elliptical rather than terete. Arrows indicate substomatal chambers (CUPC 190 — slide 31.4.1.15); × 30.
32. Xylem strand, at higher level, further attenuated. Trace to fertile branch is seen on left and protoxylem of main axis has elongated well below the level at which a second fertile branch will originate on the right (CUPC 191 — side 35.1.1.86); × 30.
33. Trace now free from xylem of main axis and becoming rectangular in shape (CUPC 190 — slide 31.3.1.151); × 30.
34. Trace to fertile branch almost enclosed by its own cortex (CUPC 190 slide 31.3.1.172); × 30.
35. Transverse section of proximal end of fertile branch system. Its xylem strand is rectangular (CUPC 190 — slide 31.3.1.80); × 30.
36. Trace in fertile branch following two dichotomies of its protoxylem strand (CUPC 190 — slide 31.3.1.2); × 30.
37. Fertile branch at higher level after xylem strand has dichotomized twice. The resulting three strands included in common cortex (CUPC 190 — slide 31.2.2.3); × 30.

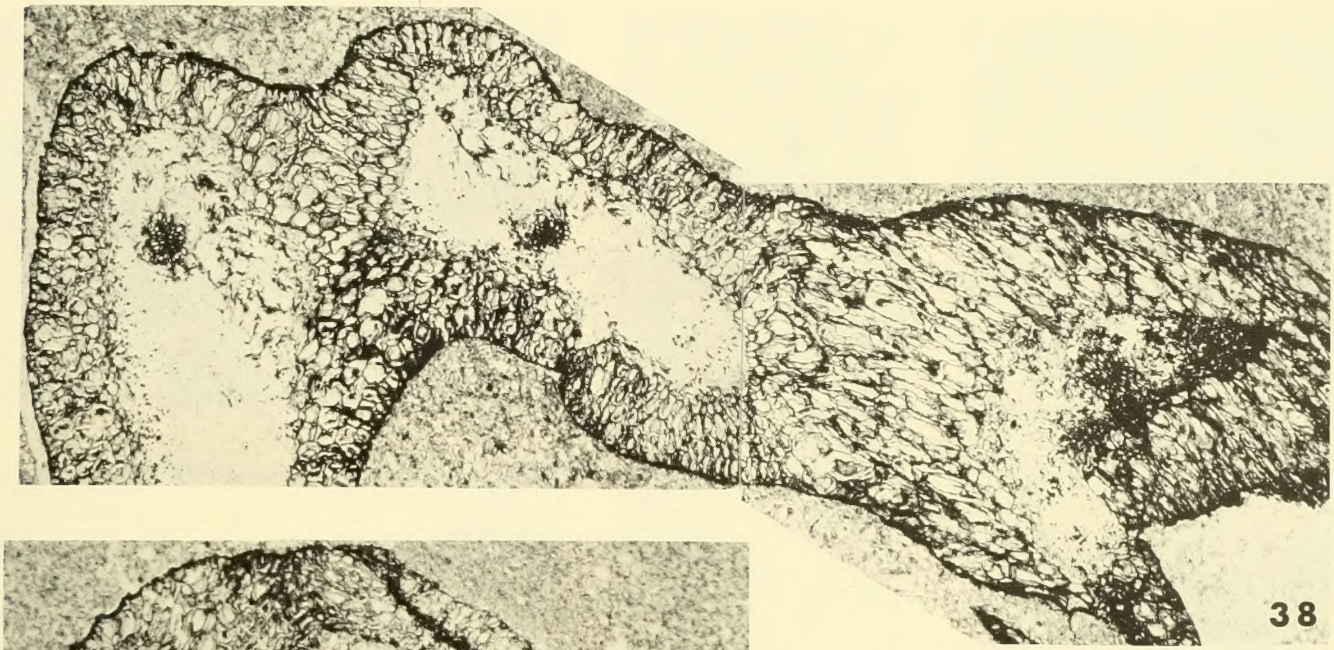
## EXPLANATION OF PLATE 21

*Figure* *Page*

38-41. *Psilophyton dawsonii,* sp. nov. .......... 105

Anatomy of lateral fertile branching system, continued from Plate 20.

38. Each of the three xylem strands produced by first "double dichotomy" now enclosed by its own cortex (CUPC 190 — slide 31.2.2.50); × 30.
39. Three branches resulting from first "double dichotomy"; middle branch already aborting. Each of the two healthy branches will repeat the stages shown in Figures 35-39, producing a second "double dichotomy". Only the final stage of this second series is illustrated for one of the two branches, in Figure 40 (CUPC 190 — slide 31.2.2.135); × 30.
40. Result of second "double dichotomy" of one of the two healthy branches in Figure 39. Here the central branch is again aborting. The fertile system now consists of four strong branches like these in Figure 40 (CUPC 191 — slide 35.1.1.59); × 30.
41. One of the four branches which were present at the level of Figure 40 is shown here with two xylem strands resulting from its first dichotomy. Each strand will soon be found in its independent cortex, and each may dichotomize three more times producing a total of 32 slender axes. Each of the 32 may dichotomize a final (fourth) time and terminate in a pair of sporangia as shown in Figures 42, 43 (CUPC 191 — slide 35.1.1.86); × 30.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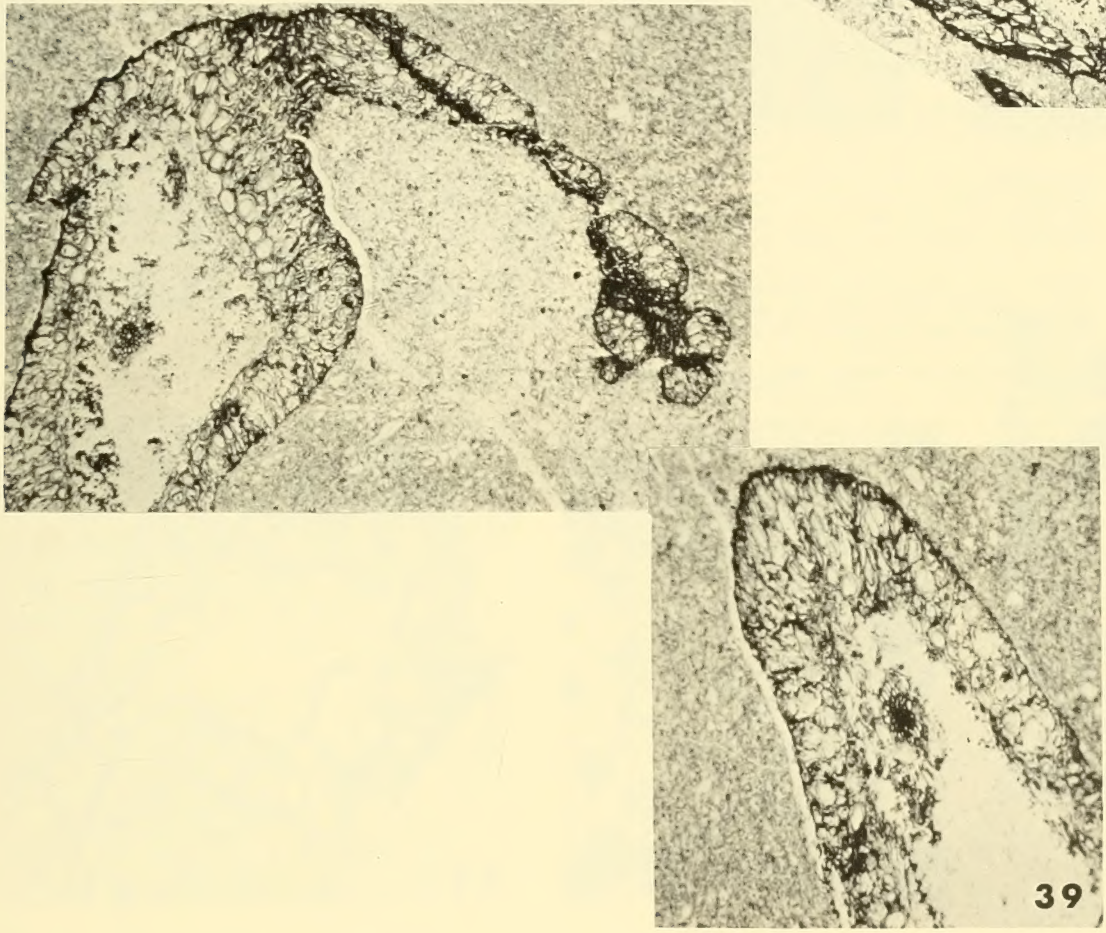
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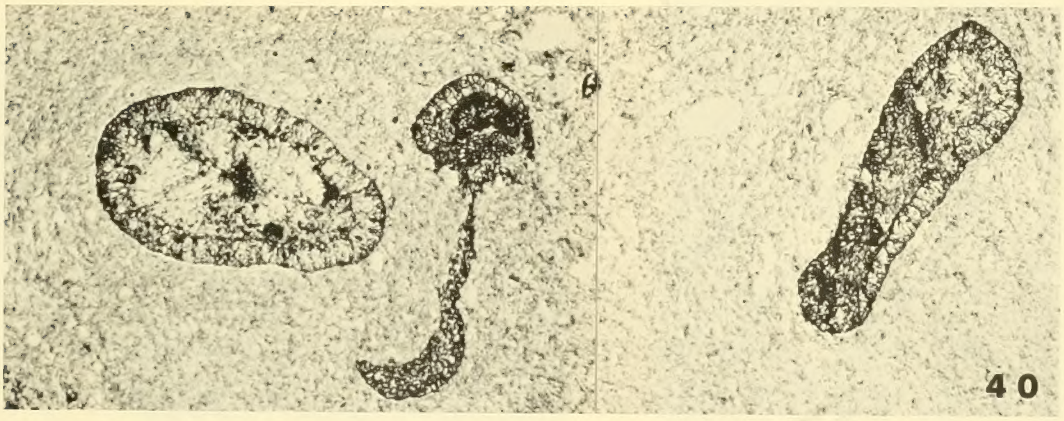
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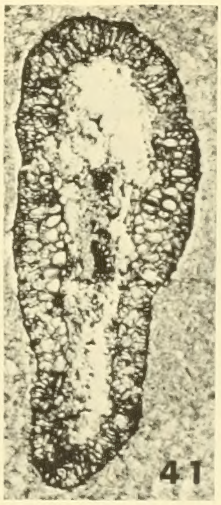
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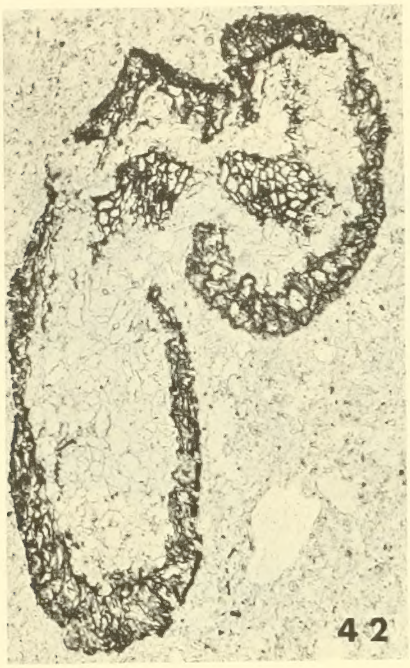
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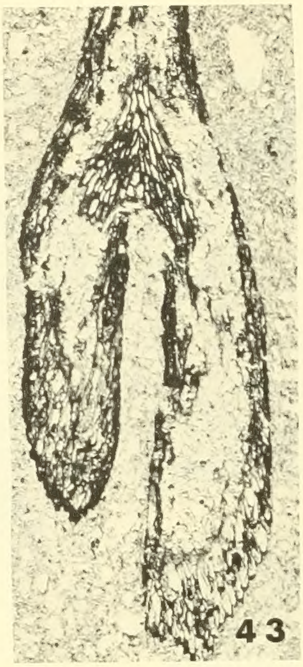
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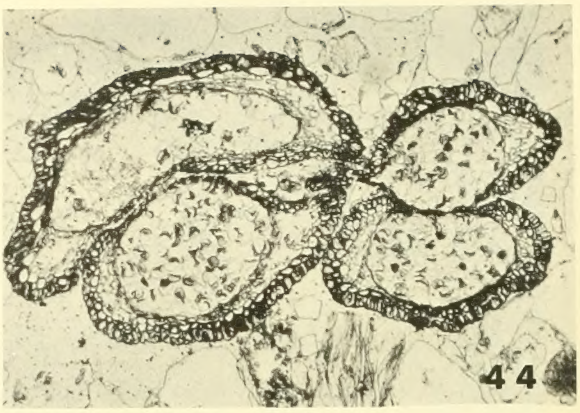
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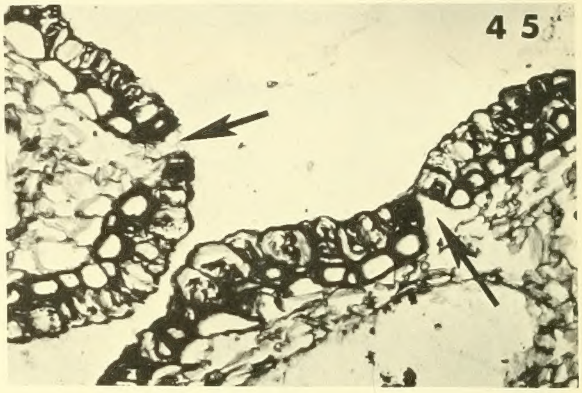
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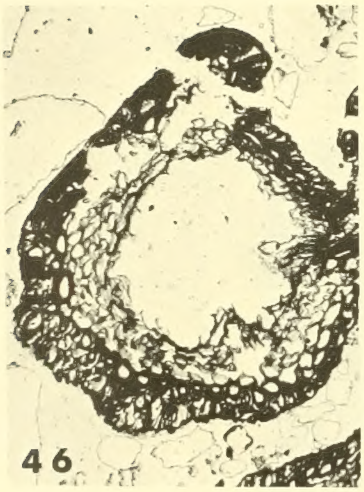
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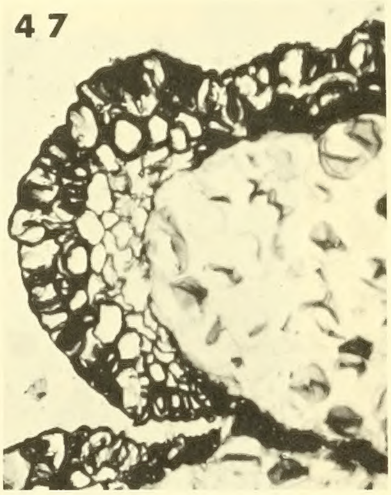
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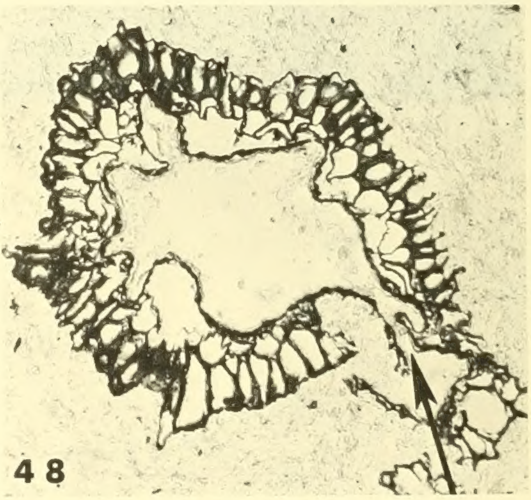
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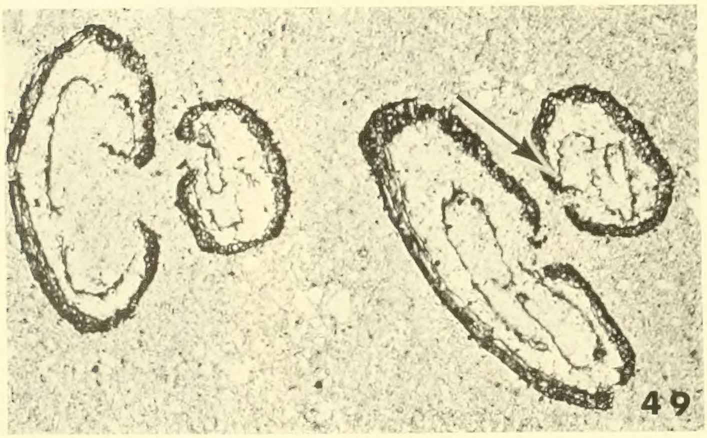
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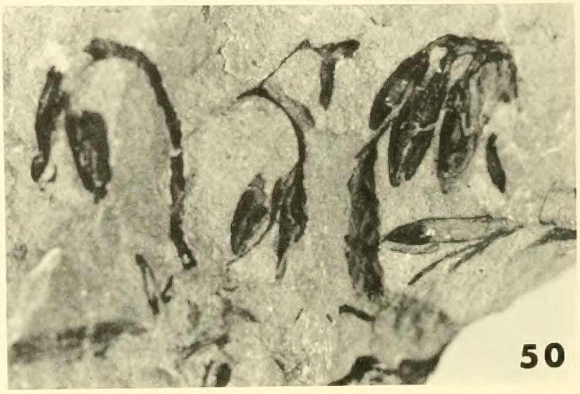
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## EXPLANATION OF PLATE 22

*Figure* *Page*

42-49. *Psilophyton dawsonii,* sp. nov. .......... 105

Structure and ontogeny of sporangia.

42. Transverse section showing the dichotomy at the base of a pair of sporangia. Note relatively massive xylem strands at this ultimate division and stem-like nature of sporangia (CUPC 194 — slide 13.23); × 70.
43. Oblique longitudinal section of a pair of sporangia showing final (sixth) dichotomy of vascular strand at base of sporangia (CUPC 191 — slide 35.2.1.34); × 35.
44. Group of four young sporangia (two pairs) containing spores and with both inner and outer "cortical" tissues still intact in some areas (USNM 175772, peel 1.1.1.2); × 30.
45. Transverse section of parts of two young sporangia, each showing a probable stoma and stomatal chamber. Parenchyma cells here are beginning to break down (USNM 175772, peel 1.1.1.2); × 90.
46. Transverse section of one entire young sporangium showing its intact outer collenchymatous and inner parenchymatous wall cells. Note resemblance to stem cortex (USNM 175772, peel 1.1.1.1); × 60.
47. One end of sporangium in Figure 44 enlarged. In this older sporangium parenchyma has broken down along much of the lateral wall but remains intact at the ends (USNM 175772, peel 1.1.1.1); × 110.
48. Mature, dehisced (arrow) sporangium. Parenchyma cells now represented only by a membrane which is formed by the innermost tangential walls of parenchyma tissue. This membrane remained inside sporangia in nature but it can be removed from the fossil by maceration as is shown in Figures 53-55 (CUPC 196 — slide 23.30); × 90.
49. Transverse section of old, dehisced sporangia. Dehiscence occurs along facing surfaces. An empty pair resembles two letter C's. Membrane remains inside sporangia, attached near line of dehiscence (arrow) (CUPC 194 — slide 13.34.)
50. Result of splitting one calcareous cobble to expose paired terminal sporangia similar to those in Figures 43-49 (CUPC 193); × 3.

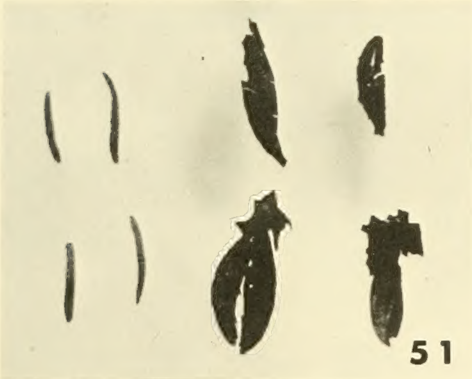
## EXPLANATION OF PLATE 23

*Figure* **Page**

51-61. *Psilophyton dawsonii*, sp. nov. .......... 105

Sporangia and spores.

51. Sporangia (right) and membranes full of spores (left) macerated out of similar sporangia. All from Abitibi River, Ontario (GSC 32720e); × 3.
52. Sporangia (Abitibi River) demineralized, embedded in paraffin and microtomed. Outer thick wall and inner translucent membrane (arrow) both visible. This is identical to the two layers found by Lang (1931, pl. 28, fig. 24 and subsequent papers) (GSC 32721); × 30.
53. Two membranes isolated by maceration from Abitibi River sporangia; one is full of spores (GSC 32722); × 60.
54. One membrane full of spores isolated by maceration from a sporangium from Douglastown (CUPC 193 — slide 1); × 35.
55. One empty membrane isolated by maceration from a sporangium from Douglastown (CUPC 193 — slide 2); × 25.
56. Single spore with uncovered, smooth exine. Remnants of envelope (? perispore) in the background outside the spore. Thickened areas along commisure have concave sides. Amb nearly circular. Some evidence of curvaturae toward lower margin (CUPC 195 — slide 21.10); × 465.
57. Mass of spores found in the matrix amongst a cluster of sporangia (CUPC 195 — slide 21.2.3); × 45.
58. One spore with its outer covering removed revealing its smooth exine. The covering envelope whose surface is granular lies to the lower left. Thickened areas along commisures have straight sides and the amb is essentially circular (CUPC 195 — slide 21.10); × 675.
59. Single spore mostly covered by envelope. Thickened triangular areas with straight sides (CUPC 195 — slide 21.2.3); × 715.
60. One tetrad in which distal and proximal walls of each spore are compressed together so that trilete mark appears to be distal in position. A. Thickened proximal wall. B. Distal wall. C. The envelope (? perispore) which separates from the spore before dispersal (CUPC 195 — slide 21.10); × 500.
61. Single spore still partially covered by envelope. Commisure split open. Thickened area with concave sides (CUPC 195 — slide 21.2.3); × 515.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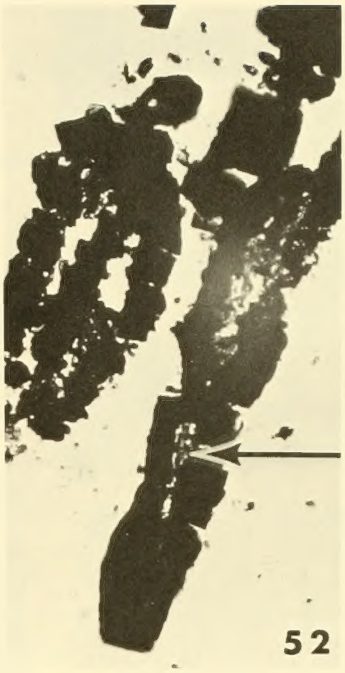
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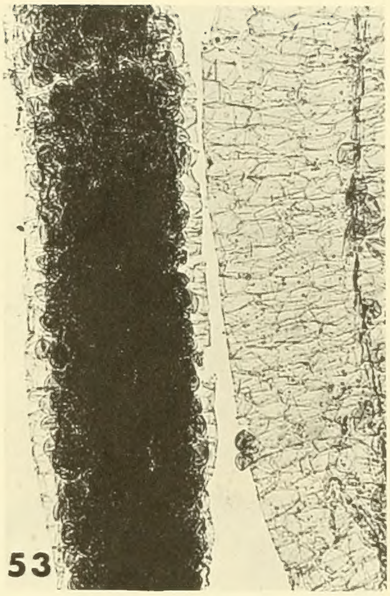
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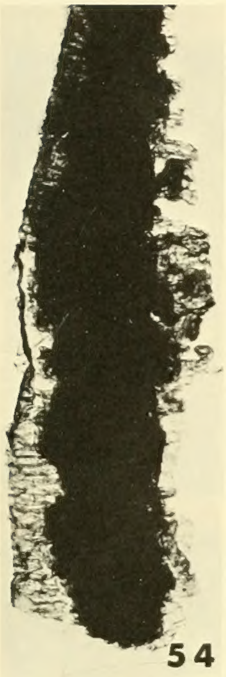
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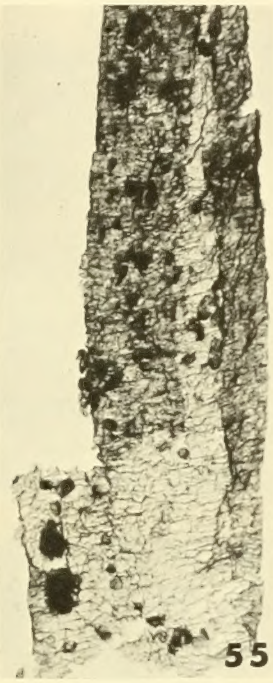
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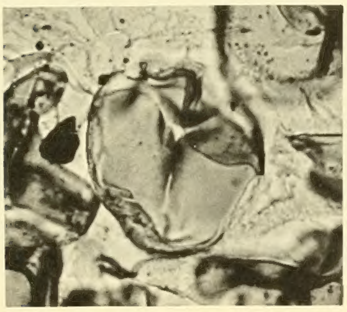
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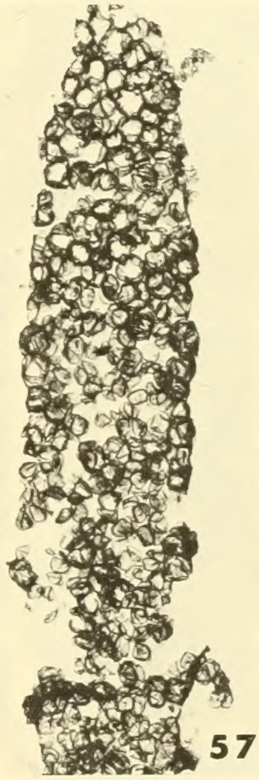
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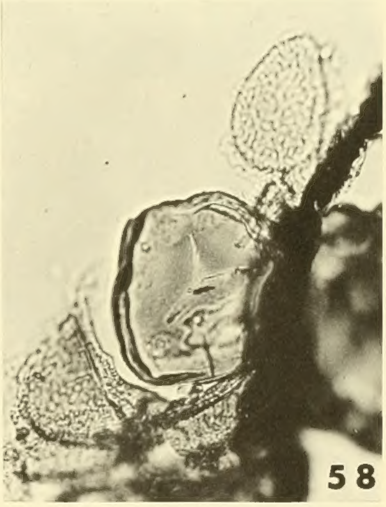
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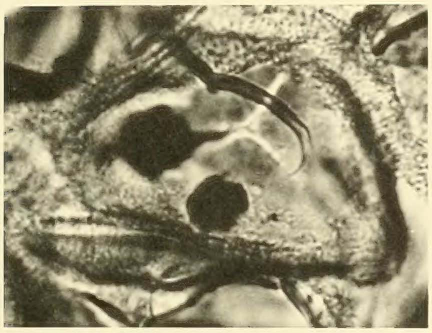
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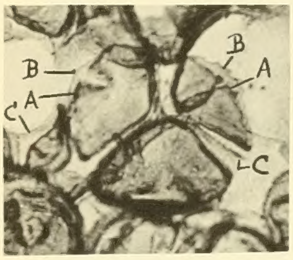

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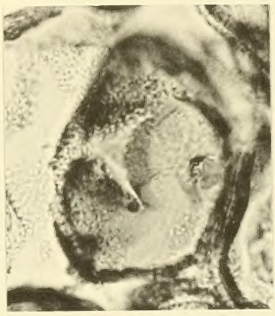
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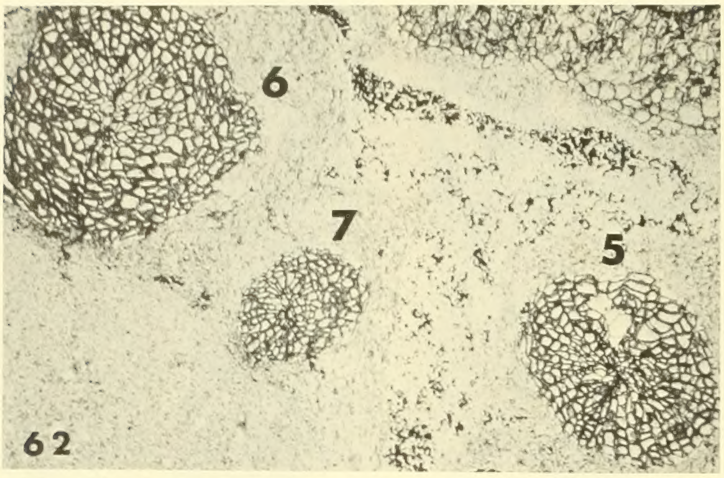

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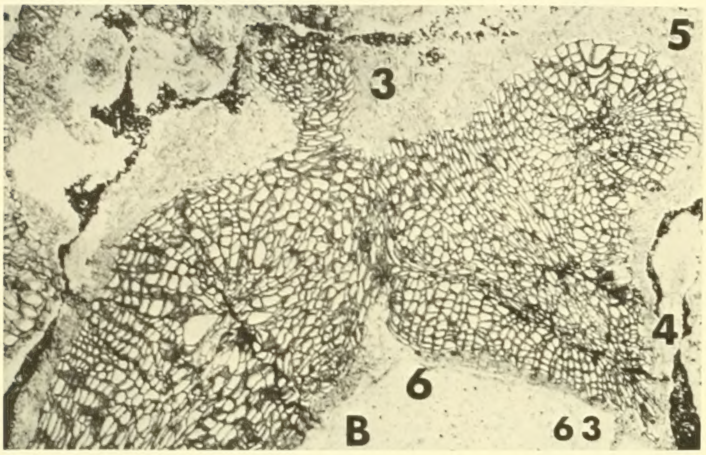

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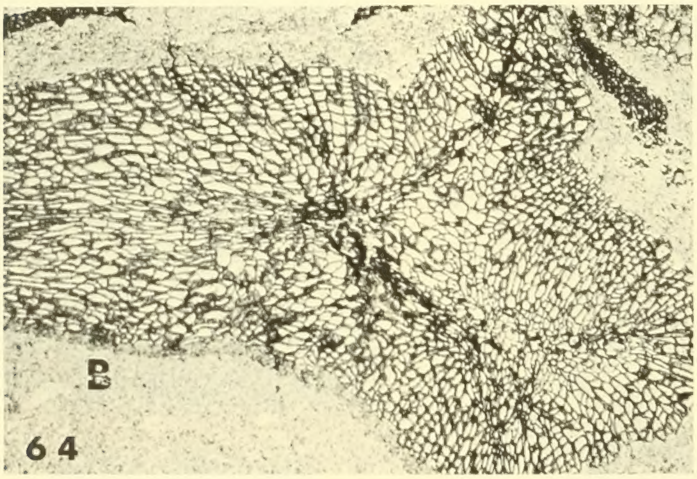

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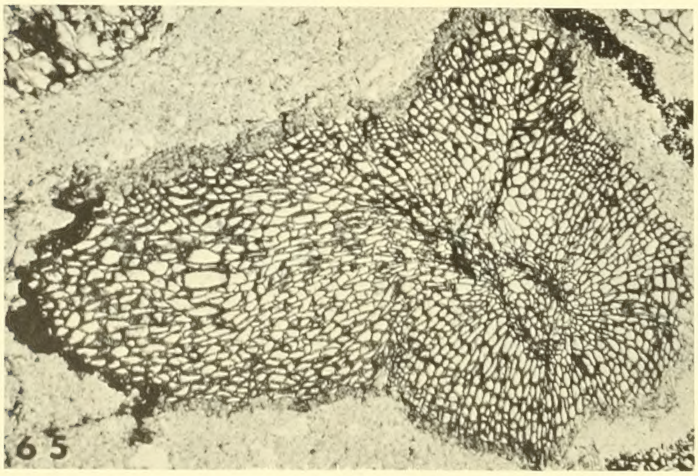

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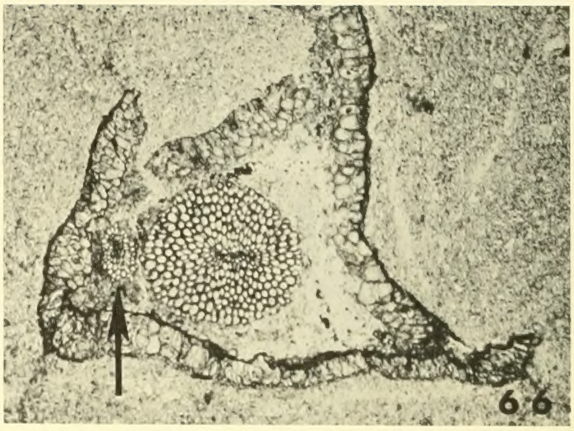

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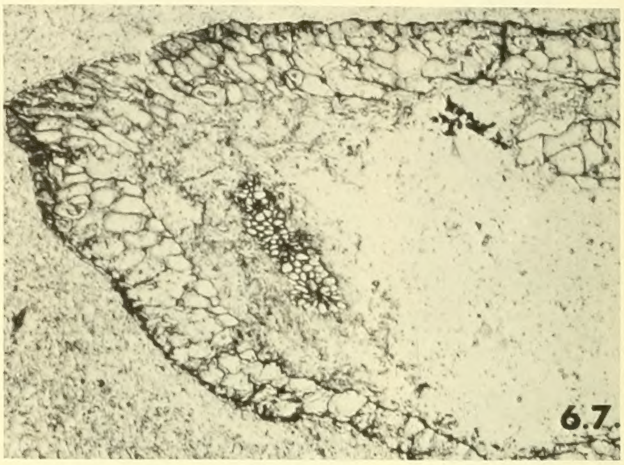

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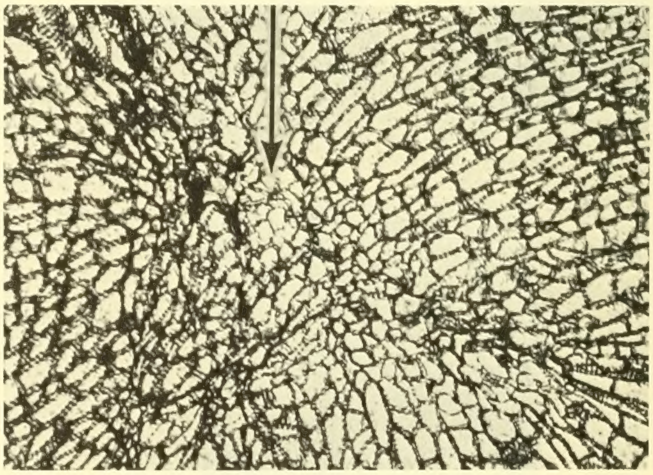

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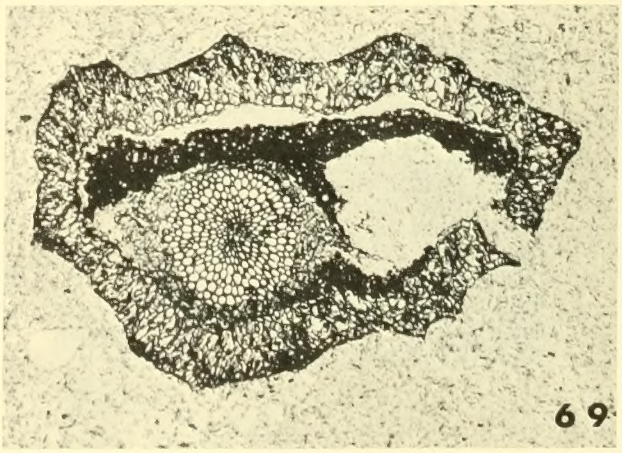

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## EXPLANATION OF PLATE 24

*Figure* *Page*

62-69. *Psilophyton dawsonii*, sp. nov. .......... 105

Anatomy of main axis in region of vegetative branching and up to the base of region of fertile branching.

62-65. Series of transverse sections from more distal toward more proximal end.

62. Vascular strands to vegetative branches 6, 7, and 5 (left to right) (CUPC 192 — slide 4.4.1.12); × 30.

63. Lower level than Figure 62: shows origin of traces to sterile branches 3, 4, 5, 6. Xylem strand of main axis B bends downward at left. Note that some metaxylem simulates secondary xylem (CUPC 192 — slide 4.4.1.14); × 20.

64. Lower level. Massive xylem strand with several large protoxylem areas. Xylem of main axis B is the large strand at left and branch 3 will be supplied by large mass at top right; remainder will eventually produce strands to branches 4, 5, 6, 7 (CUPC 192 — slide 4.4.1.16); × 30.

65. Lower level. Large compact mass of xylem. Xylem of main axis is the mass at left, branch 3 at top, and branches 4, 5, 6, 7, will originate from the remainder (CUPC 192 — slide 4.4.1.18); × 30.

66. Xylem strand of main axis B above the level of production of vegetative branches 1-7 (above Fig. 62). Note that xylem strand now resembles one about to produce a fertile lateral branch (cf. Figs. 31-33) and note the typical rectangular bundle to a fertile branch (arrow) on the left (CUPC 192 — slide 4.3.2Z.27); × 30.

67. Transverse section of rectangular bundle, first seen in Figure 66, at a higher level now with three protoxylems and about to undergo a first "double dichotomy" (CUPC 192 — slide 4.3.2Z.52); × 50.

68. Transverse section of a portion of Figure 64 to show one enlarged mass of central protoxylem (arrow) associated with the production of vegetative branches (CUPC 192 — slide 4.4.1.16); × 75.

69. Transverse section of axis, also illustrated as Figure 30, below level of production of a known fertile branch system in the holotype. Compare the size of its xylem strand with that of the central xylem in the region of vegetative branching. Figures 64, 65 taken at the same magnification. Compare its size also with the axis in Figure 66 that we suppose will produce a fertile branch system above the level of vegetative branching (CUPC 190 — slide 31.3.1.23); × 30.

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NO. 49

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# COMPARATIVE MORPHOLOGY AND SHELL HISTOLOGY OF THE ORDOVICIAN STROPHOMENACEA (BRACHIOPODA)

By

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September 9
1976

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*Library of Congress Card Number: 76-26362*

Printed in the United States of America
Arnold Printing Corporation
Ithaca, N.Y.

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# COMPARATIVE MORPHOLOGY AND SHELL HISTOLOGY OF THE ORDOVICIAN STROPHOMENACEA (BRACHIOPODA)*

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## ABSTRACT

The 44 genera of the superfamily Strophomenacea (Brachiopoda) may be arranged into a phylogeny of four families. The family Oepikinidae, which contains the oldest species of the superfamily, possesses archaic characters including fine pseudopunctae, subrectangular to prolate shape, plano-convex to concavo-convex profile and prominent dorsal septa. The family Leptaenidae diverged from the oldest oepikinids by acquisition of coarse pseudopunctae, prominent geniculation, and rugae. The Leptaenidae subsumed the subfamilies Murinellinae, *nov.*, with prominent dorsal septa, Leptaeninae, without prominent dorsal septa, and Leptaenoideinae, with cemented habit. The family Rafinesquinidae originated from early oepikinids by loss of dorsal septa and acquisition of coarse pseudopunctae. The family Strophomenidae arose from the oepikinids with the development of a biconvex, flattened, or resupinate profile. The Strophomenidae subsumed the subfamilies Furcitellinae, with evident dorsal septa and unusual shell shapes and profiles, and Strophomeninae, with strong resupination and obscure dorsal septa.

Many morphological structures underwent modification throughout the history of the Strophomenacea. The shape and profile of the valves, size of pseudopunctae and form of the teeth and diductor muscle scars are taxonomic differentia at the familial level. The pseudodeltidium, chilidium, pedicle foramen and dorsal septa underwent parallel evolution in the various families. The cardinal process displays poorly defined taxonomic differentiation and parallel evolution. The profile of the valves, dental lamellae, muscle bounding ridges and socket buttresses underwent collateral changes which are indicative of interrelationship. The adductor muscle scars, posterior platform, meso-cardinal ridge, vasculae, radial prosopon and size of species have little taxonomic or evolutionary significance.

A revised shell-layer nomenclature for brachiopods is proposed to replace standard terminology which is either inappropriate or ambiguous. The shell-layers are, from external to internal surface, the periostracum, the outer carbonate layer (primary layer of authors), inner initial layer (secondary layer of authors) and secondary deposits. Microstructural designations may be substituted for these layer-names in reference to specific brachiopod groups.

Strophomenaceans do not possess evidence of periostracum. The outer carbonate layer is a dark lamellar layer on the disk of the valves and a thick microcrystalline layer on the palintrope. The pseudodeltidium and chilidium are continuations of the microcrystalline layers of the palintropes. The microcrystalline layers of the palintropes are folded complexly along the sides of the denticular plates and into the sockets. The inner initial layer is pseudopunctate lamellar tissue which forms most of the bulk and morphological features of the valves. The denticular plates and socket plates are composed of specialized inner initial tissue. The inner initial tissue of the dental lamellae is not separated from the palintrope or floor of the valve by sutures. The pedicle conduit penetrates the inner intial tissue at the apex of the ventral valve. The secondary deposits are limited generally to the muscle scars and cardinal regions of the valves. The structure of the secondary deposits of the muscle scars is complex. The myophores of the cardinal process are formed of cancellus secondary deposits. A spondylium triplex and a hemisyrinx are formed of secondary deposits in the apex of the delthyrial cavity of a few species.

All strophomenaceans are pseudopunctate; most bear taleolae. Fine pseudopunctae are randomly dispersed in oepikinids and strophomenids and coarse pseudopunctae are geometrically positioned in rafinesquinids and leptaenids. In general, there is an inverse relationship between the diameter and packing density (number per unit area) of taleolae.

Evidence suggests that those strophomenaceans which possess a sealed pedicle foramen in adulthood probably rested upon the concave valve during life.

## INTRODUCTION

The articulate brachiopods of the Order Strophomenida Öpik flourished from Lower Ordovician throughout the rest of the Paleozoic Era. The order diminished in early Mesozoic time and reached extinction in the Jurassic if the taxonomically perplexing thecideoids (Triassic to Recent) are excluded. The order as it is understood today subsumes more genera than any other order of the Brachiopoda. No other order of brachiopods exceeds the Strophomenida in morphological diversity or ecological adaptations.

The four suborders and nine superfamilies of the Strophomenida form a related continuum but their extreme diversification precludes the possibility of a succinct, unequivocal diagnosis for the entire group. Most of the strophomenids possess pseudopunctate shell structure. The valves generally have wide hinge lines and concavo-convex, less commonly resupinate or biconvex, profiles. Generally, a supra-apical pedicle foramen in the juvenile shell, a pseudodeltidium and a chilidium are present. The cardinal process is rarely absent but this structure may be varied in form. There is rarely a prominent or elevated structure for support of the lophophore. The Order Strophomenida differs from all other orders by the combination of these characters but not one character is unique to the order or invariably present.

The order Strophomenida is divided into the suborders Strophomenidina Öpik, Chonetidina Muir-Wood, Productidina Waagen and Oldhaminidina Williams. The Strophomenidina (Ordovician to Triassic) includes the oldest and least specialized species of the order. There is no unique and ubiquitous character which distinguishes the Strophomenidina from the related suborders. The Strophomenidina has the characters of the order but lacks the hinge spines of the Chonetidina, the excessively concavo-convex or conical profile and the hollow spines of the Productidina and the slotted internal plate and oyster-like shape of the Oldhaminidina.

This study concerns the superfamily Strophomenacea King which is one of five superfamilies of the Strophomenidina. The other superfamilies are the Plectambonitacea Jones, the Christianiacea Williams, the Stropheodontacea Caster and the Davidsoniacea King (= Orthotetacea Waagen). The oldest species of the Strophomenacea are early Middle Ordovician in age. Strophomenaceans occur in great number and diversity in rocks of Middle and Upper Ordovician age. Of the four families of strophomenaceans, the Oepikinidae Sokolskaya became extinct in the Upper

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*A dissertation submitted to The Graduate School of the University of Cincinnati in partial fulfillment of the requirements for the degree of Doctor of Philosophy 1966.

Ordovician, the Rafinesquinidae Schuchert and Strophomenidae King continued in reduced numbers into the Silurian where they became extinct and the Leptaenidae Hall and Clarke ranged into the Mississippian.

The Plectambonitacea (Lower Ordovician to Devonian) incorporates the oldest species of the Strophomenidina and in many respects possesses the fundamental morphological characteristics of the suborder. As is the case in many ancestral stocks, certain structures of the Plectambonitacea are so diversely formed that if the variations were present in later stocks the variations would constitute major taxonomic differentia. For example, the cardinal process of the plectambonitaceans is either absent, a single blade, or trifid. The cardinal process of the other superfamilies is bifid.

The Strophomenacea is an evolutionary derivative from the Plectambonitacea. Unfortunately, the Plectambonitacea is not known in sufficient detail to permit a more specific judgment of the source of the Strophomenacea. The Stropheodontacea and Davidsoniacea are derived from the Strophomenacea; the origin of the Christianiacea is unresolved. The Strophomenacea is differentiated from the Plectambonitacea by the character of the cardinal process. The simple teeth of the Strophomenacea are absent from the Stropheodontacea and in their place occur rows of denticles along the hingeline. The Strophomenacea and Christianiacea are differentiated most readily by the shape, profile, and prosopon of the valves. The valves of the Strophomenacea have the shape of a shield. The profile of the valves is flattened to moderately concavo-convex or resupinate. The prosopon of the external surfaces is distinctly costellate. The valves of the Christianiacea are much longer than wide and are deeply concavo-convex. The Christianiacea has only faint traces of external prosopon. The Davidsoniacea is not so easily differentiated from the Strophomenacea as are the other superfamilies. Few species of strophomenaceans lived cemented to any object on the sea-floor. The posterior platform in the dorsal valve is a prominent structure of the Strophomenacea. The simple teeth generally are supported by dental lamellae. The lobes of the cardinal process are disjunct or barely fused (conjunct) at the posterior. In contrast, most species of the Davidsoniacea lived cemented to an object on the sea-floor. A posterior platform and dental lamellae generally are absent and the lobes of the cardinal process commonly are completely ankylosed to form a shelflike structure. A more detailed justification for the novel superfamilies Christianiacea and Stropheodontacea is presented in the introduction to the section on Systematic Paleontology.

The object of this study is to document and clarify the morphology and shell histology of the Ordovician strophomenaceans. No comprehensive analysis of the entire superfamily has been published. Those works which treat taxonomically, stratigraphically, or geographically restricted portions of the superfamily contain some unresolved discrepancies in observation, interpretation, and terminology. In the course of the work, over 1300 peel sections and 1400 photographs were made. The extensive collection of Ordovician strophomenaceans in the United States National Museum as well as collections and specimens from other museums were studied. It is hoped that this work may be useful in consolidating and expanding the understanding of strophomenacean morphology and histology.

Early in the course of study it became apparent that the taxonomy of the Strophomenacea required revision. Neither morphological or histological studies could be rationally pursued without a detailed taxonomic framework to guide the investigation. The sections on Systematic Paleontology and Phylogeny are the result. Taxonomy was not a goal of this study but a necessary and hopefully significant adjunct to the study.

Genera are not diagnosed or described in the section on Systematic Paleontology. The genera are clearly diagnosed and illustrated in the recently published (November, 1965) *Treatise on Invertebrate Paleontology, Part H, Brachiopoda,* hereafter called the *Treatise.* Additional excellent contemporary descriptions and illustrations of most strophomenacean genera appear in Cooper (1956) and Spjeldnaes (1957). Fortunately, these works permit the laborious and voluminous descriptions and illustrations to be omitted. Several new genera have been recognized in the course of the study. These do not add significantly to the descriptions or ranges of the families of the Strophomenacea nor do they evidence new taxa of familial rank. Inasmuch as manuscript names do not have formal status or protection under the International Code of Zoological Nomenclature and these genera do not add significantly to this study, the newly recognized genera are neither named nor described.

Most of the taxa within the order Strophomenida have been the subjects of contemporary, comprehensive studies. The record includes the works of Williams (1953) on the Stropheodontacea and Oldhaminidina, Elliot (1958), on the enigmatic Thecideidina, Muir-Wood and Cooper (1960) on the Productidina and Muir-Wood (1962) on the Chonetidina. Only the Plectambonitacea, Strophomenacea, and Orthotetacea have not received a detailed comprehensive study in recent years. It is hoped that this investigation to some extent will contribute to our understanding of the Strophomenacea.

## TECHNIQUES

The nature of strophomenacean brachiopods has required development of several novel preparation techniques. These include techniques for the study of pseudopunctae, for preparation of thin sections and peel sections, and for removing matrix from brachiopods.

Pseudopunctae may be observed on the external and internal surfaces of strophomenacean valves. The number and arrangement of pseudopunctae near the internal surface is controlled and obscured by secondary deposits. It is more practical to count pseudopunctae on the external surface of the valve for an accurate determination of their packing density in the inner initial layer. Not all pseudopunctae, however, reach the external surface of the inner initial layer. Moreover, some areas of the external surface of the valves may be covered by outer carbonate layer, which is not penetrated by pseudopunctae, or by matrix and some areas may be bruised or abraded.

The packing density of pseudopunctae may be computed easily from counts made upon tangential peels. The planar tangential peels can pass through only one small area of a curved brachiopod shell. Brief etching of the entire external surface of a valve is more practical than fabrication of tangential peels. Complete etching permits packing densities to be computed for several regions of a valve for comparison.

Brief etching in acid causes pseudopunctae to become prominent pits in the shell surface. Etching also removes the outer carbonate layer, thin matrix deposits and obliterates bruises and scratches. The surface of the valve is cleaned and polished after etching. Counts of pseudopunctae may be made directly from the shell surface under a microscope with a calibrated grid reticle. Valves are etched satisfactorily in 0.85N[1] acetic acid for 10 to 20 minutes depending upon shell thickness. This technique is not recommended for rare or exceptional specimens and, of course, renders specimens unsuitable for photography or display.

Tangential peels are useful for measuring the diameter of taleolae. Details of the preparation of peels are furnished in the paragraphs on serial sectioning to follow. The center of the external surface of the ventral valve is ground to a flat surface for preparation of a tangential peel. The surface is ground until the visceral cavity is reached. The taleolae to be measured occur about halfway between the center and the edge of the ground surface, that is, taleolae diameters are measured at approximately the middle of the inner initial layer. Taleolae diameters are measured with an accurately calibrated, finely divided reticle at high magnification (×100).

Only longitudinal thin sections of strophomenaceans can be made by conventional techniques. Transverse and sagittal sections require special preparation. The shell material flakes away if a sagittal or transverse edge of a specimen is ground in the conventional manner upon a rotary lap or a glass plate. Shell material is too impermeable to impregnate with Canada balsam or Lakeside 70. Specimens were invested in plaster compounds with hope that the plaster would prevent spalling of tissue. Plaster is brittle and does not adhere well to the surface of the specimens. Specimens were invested in polyester resin plastics[2] with limited success. Polyester resins bond tightly to specimens, were and could be ground with ease. Unfortunately, polyester plastic warped and became flexible at the temperature needed to cement the ground surface to a glass slide with Lakeside 70 (145° C.). Several brands of epoxy cement were used for bonding the lapped surface to glass microscope slides. The epoxy bond was satisfactory but all epoxy cements that were tried have bubbles and fibrous structure or objectionable flow-structures after polymerization. The cover glass was mounted with cold setting Permount[3]. Slides made by this method are satisfactory for study but are not adequate for published illustrations.

Closely spaced, serial thin sections of brachiopod shell cannot be made with commonly available equipment. Closely spaced, serial peel sections may be made quickly and easily with parallel grinding instruments as those described in the *Treatise* (p. H253). Peel sections are well suited for studies of brachiopods in which it is necessary to follow changes of morphology and histology of structures.

Peel sections were prepared by grinding a surface into a specimen with fine abrasive, etching the ground surface in acid and replicating the etched surface in transparent plastic. The process works because a crystal of calcite (and other anisotropic crystals) etches at different velocities in different crystallographic directions. A ground and etched surface through a brachiopod shell has topographic relief which is determined by the crystallographic orientation of the calcite plates, fibers and granules of which the shell is constructed. The plastic replica has a frosted, translucent appearance except in areas where the plastic incorporates insoluble grains of opaque matrix which have been liberated by etching. The peel section of the fossil has the appearance of a thin section in phase contrast illumination because the surface of the plastic acts as a fine diffraction grating. Histological differences in the shell are more apparent in peel sections than in thin sections.

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[1] 0.85 N acetic acid may be made by mixing 1 part 17N C.P. glacial acetic acid (from the bottle) with 19 parts water.

[2] Polylite (8237), Reichhold Chemicals, Inc., White Plains, New York. E-Z Cast, Clear Polyester Casting Resin, Industrial Arts Supply Co., Minneapolis, Minnesota.

[3] Fisher Scientific Co., Fair Lawn, New Jersey.

Transverse peel sections of brachiopods are most useful because every structure in a transverse peel section is symmetrical or paired. It is easy to locate the position of a transverse section on a whole specimen to which it is compared.

Serial sections for this study were ground with a modified Simpson serial section machine[4]. A Simpson serial sectioning machine permits faster but less accurate grinding than a Croft parallel grinder. Nevertheless, grinding error with a Simpson serial sectioner is ±0.002 inches which is less than the depth of etching.

Preparation of peel sections was outlined by Boardman and Utgaard (1964). Their procedure is unnecessarily complicated for brachiopod studies and is modified as follows:

(1) Make a carefully oriented, transverse cut with a diamond saw through the anterior end of a brachiopod specimen. Cut several specimens of the same species. Stand the specimens on the cut surface in a square metal mold or a glass ring[5]. Very small specimens may be held in a small pyramid of modeling clay. Leave at least ¼ inch (about 5 mm) space between the specimens. Be careful to orient all specimens in the same way for convenience in later study. Stand several automatic pencil graphite "leads" in modeling clay pyramids near the edges of the mold. The spots made by the "leads" will serve as indicator marks in the finished series of peels.

(2) Invest the specimens in polyester resin[6]. Remove the plastic block from the mold.

(3) Grind the top of the plastic block to a flat surface and cement the top with epoxy resin to a holder of the serial section machine.

(4) Affix the holder and plastic block to the serial section machine. Grind with coarse abrasive on a rotary lap to a desired surface in the brachiopod specimens. Grinding should proceed from anterior to posterior.

(5) Record the setting of the serial section machine. Remove the holder and plastic block and finish the surface on a glass plate with number 600 grit abrasive. It is not necessary to polish the surface with tin oxide as Boardman and Utgaard indicated because etching polishes the surfaces of the specimens and removes the scratches produced by the fine grinding.

(6) Etch the finished surface for 20 seconds in 0.6N hydrochloric acid. Comparative tests show that hydrochloric acid produces a finer surface than acetic or formic acid. During etching, agitate the specimen to dislodge bubbles and to prevent unequal etching. Let the plastic block and specimens dry thoroughly. Do not touch the etched surface.

(7) The peel is made in 0.06 inch thick cellulose acetate sheet stock[7]. Cut the cellulose acetate sheets into pieces twice as large as the ground surface of the plastic block. A large border around the peel sections minimizes warping of the plastic sheet.

(8) Immerse the ground surface of the plastic block in acetone. Drip acetone onto the cellulose acetate slide to form a puddle larger than the ground surface of the plastic block. Acetone must not flow onto the underside of the cellulose acetate sheet. Press the ground surface of the plastic block into the cellulose acetate sheet and place a small weight (3 lbs. is satisfactory) on the plastic block. This step of the process must be done quickly because acetone evaporates rapidly. Both surfaces must be wet with acetone or bubbles will occur in the peel. Too much weight on the plastic block will cause the cellulose acetate sheet to warp. Contrary to Boardman and Utgaard, some weight on the plastic block seems to be necessary unless the specimen holder is heavy.

(9) Allow the acetone to evaporate for at least 30 minutes. Long periods of drying (overnight) do not cause damage.

(10) Snap the plastic block from the cellulose acetate sheet. Rub one border of the slide with a coarse typing eraser. Label the slide in this area with drawing ink and cover the label with clear lacquer.

(11) Replace the plastic block and holder in the serial

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[4] G. G. Simpson, A simplified serial sectioning technique for the study of fossils. Am. Mus. Novitates 634, June 10, 1933.

[5] Glass rings may be made by cutting small vials with a diamond saw. Place the glass ring on a sheet of glass and seal the edge with modeling clay. Metal molds are available from Ward's Natural Science Establishment, Inc., Rochester, New York.

[6] Polylite (8237) Reichhold Chemicals, Inc., White Plains, New York, has been found to be excellent. Unlike other plastics, Polylite (8237) has a Mohs hardness of 3, is acetone and acid resistant and does not smear when ground.

[7] Obtainable from the Transilwrap Company of Cleveland, Inc., Cleveland, Ohio.

section machine. Adjust the serial section machine to the desired depth of grinding. Grind a new surface. Repeat the entire operation.

Conventional methods of cleaning brachiopod specimens with steel needles and potassium hydroxide pellets may injure specimens. Hard matrix may require these cleaning methods as a last resort. Matrices which contain clay may be removed by immersing the specimen in 30% hydrogen peroxide. The hydrogen peroxide will cause the clays to oxidize, expand and soften. Transfer the specimen to an ultrasonic cleaner[8]. The ultrasonic cleaner will remove most clay deposits but leave sand grains upon the surface of the specimen. The sand grains can be removed under a microscope with a needle or brush. The procedure can be repeated as many times as necessary. Use 30% hydrogen peroxide with caution; it is extremely caustic and potentially explosive.

All photographs for this study, except those taken by the Audio-Visual Service, Miami University, Oxford, Ohio, have been made with a 35 mm, single-lens reflex camera, equipped with a 55 mm lens. Photographs were made on Eastman Kodak, High Contrast Copy film, developed in Dektol and printed on Polycontrast paper. All specimens were coated with ammonium chloride sublimate for photography. Specimens were backlighted with a portable light table to obviate close cropping of each photograph. Dark field illumination is advantageous for photography of peel sections.

## ACKNOWLEDGMENT

The study and research for this dissertation was conducted during graduate study at the University of Cincinnati, Department of Geology, 1956-1960, and while an Instructor of Geology at Miami University, Oxford, Ohio, 1960-1966. The support, encouragement and facilities offered by the faculties and administrations of both institutions are sincerely appreciated. Professor Kenneth E. Caster supervised this study. His guidance and interest is acknowledged with deep gratitude and respect. G. Arthur Cooper, Director of Paleobiology, United States National Museum, provided generous counsel and made available for study the extensive brachiopod collections of the National Museum.

I am indebted to the following persons for valuable advice and specimens for this investigation: G. Winston Sinclair, Geological Survey of Canada; Alwyn Williams, Queens University of Belfast; Nils Spjeldnaes, Paleontological Institute, University of Oslo; Arthur J. Boucot, California Institute of Technology; and Robert B. Neuman, United States Geological Survey. Additional specimens were loaned by the curatorial staffs of the American Museum of Natural History, New York State Museum and Science Service, and the Walker Museum of the University of Chicago. Mr. Jess Merida of the National Museum provided helpful instruction in the preparation of peel sections.

The staff of the Audio-Visual Service of Miami University gave valuable guidance in the preparation of illustrations. Their prompt, proficient photographic assistance is appreciated. This manuscript was proofread and typed by my wife, Gracia T. Pope. My continuing thanks go to her for her encouragement and help.

In the explanations to illustrations, the abbreviations USNM and MU signify the United States National Museum and the geology museum of Miami University.

## ORIENTATION AND GENERAL MORPHOLOGY

### TERMINOLOGY OF ORIENTATION AND DIRECTION

The general terminology of orientation of articulate branchiopods, as anterior, posterior, dorsal and ventral, is adequately understood and will not be reviewed. It should be noted that the description by Percival (1960) of orientation during the larval development of *Notosaria nigricans* (G. B. Sowerby I) reverses his earlier observations (1944) of orientation during the larval development of *Terebratella inconspicua* (G. B. Sowerby I). Consequently, descriptions of brachiopods may again include reference to dorsal and ventral valves without explanation and the cumbersome and commonly inappropriate terms, pedicle valve and brachial valve, may be retired.

There is a definite need for a more rigid discipline of terminology concerned with directions in brachiopods, especially the directional terminology applied to structures on the internal surfaces of the valves. Even in published descriptions of recent date, it is not uncommon to find directional terms so ambiguously employed that authors' meanings are clear only by reference to illustrations. Text-figure 1 illustrates some of the recommendations which follow. For brevity, only those terms which are new in this study or commonly subject to misuse or ambiguous application are discussed.

It is convenient to imagine a brachiopod set into a rectangular prism as in Text-figure 1, A, B, C, for definition of directions. It may be seen in the text-figure that "anterior",

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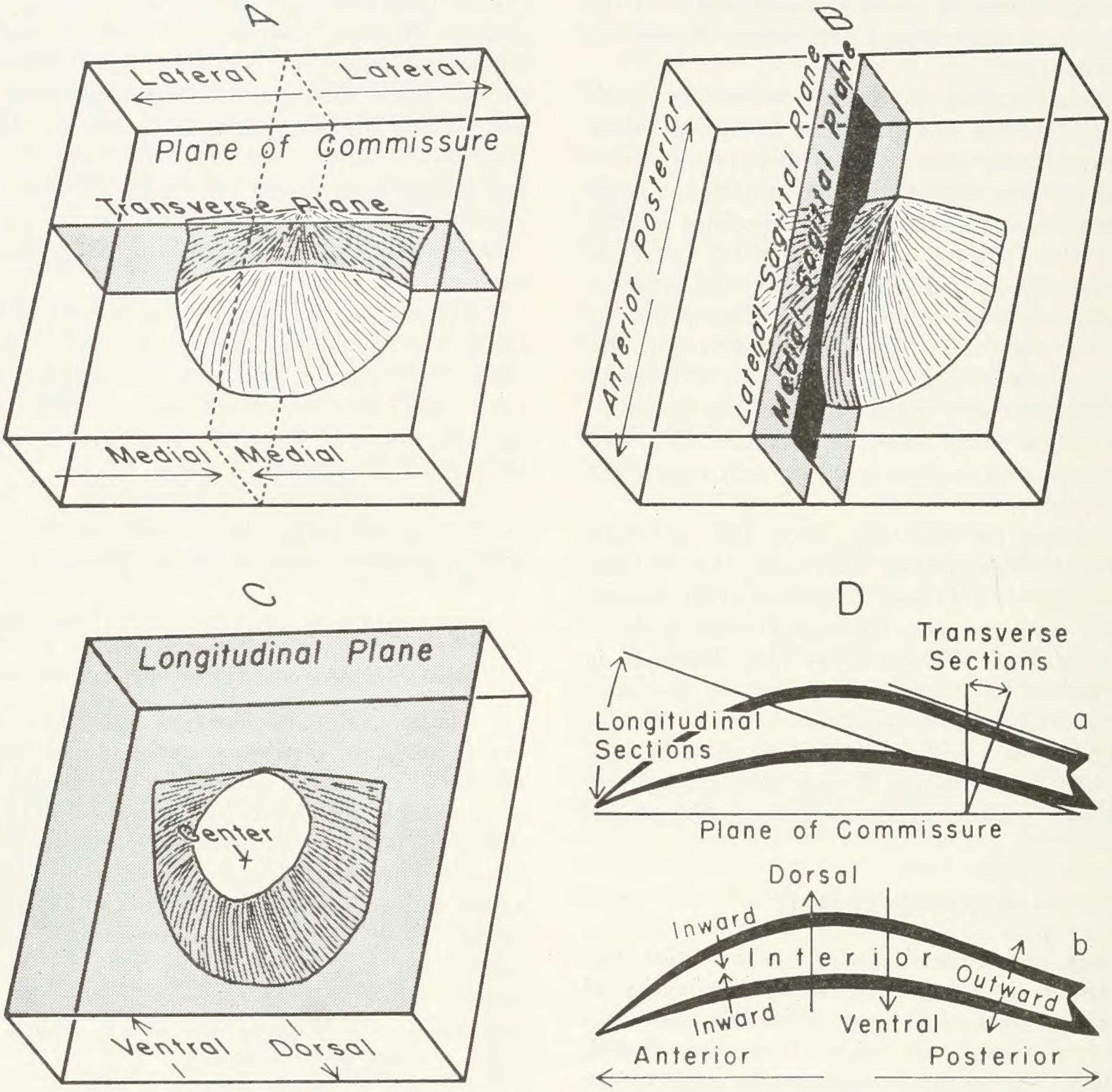
[8] The ultrasonic cleaner that has been used successfully has a maximum output of 100 watts at 40 kilocycles frequency.



*Text-figure 1.*—Planes, sections, and directions in brachiopods. A and B. Transverse and sagittal planes. C. The clear area in the center is an arbitrary point along the medial axis about midway be-longitudinal plane (top surface of block) and the brachiopod. The center is an arbitrary point along the medial axis about midway between the anterior and posterior extremes of the branchiopod. D-a. The direction of longitudinal sections may vary from parallel to the plane of commissure to parallel to the external, posterior surface of a valve. The upper limb of the angle of longitudinal sections is parallel to the line above the external, posterior surface of the dorsal valve. Transverse sections are normal to longitudinal sections.

"posterior", "dorsal" and "ventral" may be used as positional terms (the anterior), and as directional terms (toward the anterior).

Another set of directional terms is needed in addition to anterior, posterior, dorsal, and ventral. This set of directional terms is "medial" and "lateral". The plane of bilateral symmetry is a sagittal plane which divides the brachiopod into mirror-image halves. The plane of bilateral symmetry corresponds to the medial saggittal plane. "Medial" is preferred to "median", although the latter is customary, because of the established usage of "median" in statistics and because the adjective "medial" combines more euphoniously with most nouns. Structures included in the medial sagittal plane have a medial position. Structures which face or are directed toward the medial sagittal plane have a medial direction. "Lateral" is used to indicate the direction or position away from the medial sagittal plane. "Dorsad", "ventrad", "mediad" and "laterad" are convenient abverbial forms of these terms.

Most structures of brachiopods are oriented at an angle to the anterior-posterior, dorsal-ventral and medial-lateral directions. It is necessary commonly to combine directional terms to describe the orientation of oblique structures. For example, the surfaces of muscle bounding ridges which converge toward the posterior may be called the anterior-medial surfaces and the posterior-lateral surfaces. If structures converge or diverge, as in the example, the direction of convergence or divergence must be specified or clearly understood.

A brachiopod valve has an "internal surface" and an "external surface". The space between articulated valves is the "interior". There is no "interior surface" and no "exterior surface". The internal surface is called the "floor" of the valve by some authors. Use of "floor" in this manner should be suppressed because if one imagines articulated valves the floors face one another. "Floor" may be used for restricted areas of the internal surfaces of valves, as the "floor" of the delthyrial cavity or the "floor" of the umbonal chamber, because there is no satisfactory substitute term.

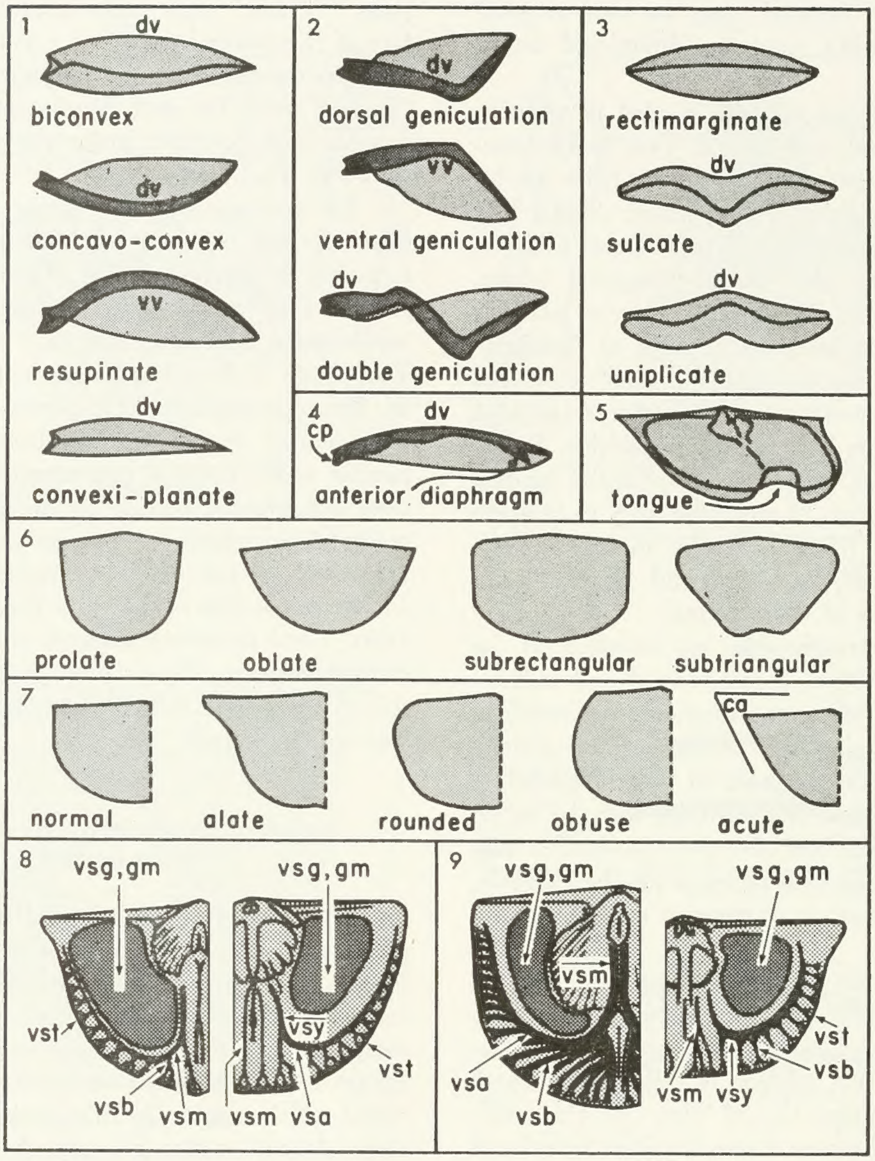
The words "in", "out," "inner", "outer", "inside" and "outside" should be avoided in description of orientation and direction of structures. These words are difficult to apply without ambiguously meaning either the medial to lateral direction or the dorsal to ventral direction. "Inward" and "outward" may be used with caution, as shown in Text-figure 1, D-b to indicate direction across the thickness of one valve.

"Middle" is a meaningless term with respect to brachiopods. "Middle" may mean medial, the interior, the surface of the visceral cavity of a valve or a position midway between the posterior and anterior along the medial plane. "Center" may be used for the position midway between anterior and posterior along the medial sagittal plane as shown in Text-figure 1, C.

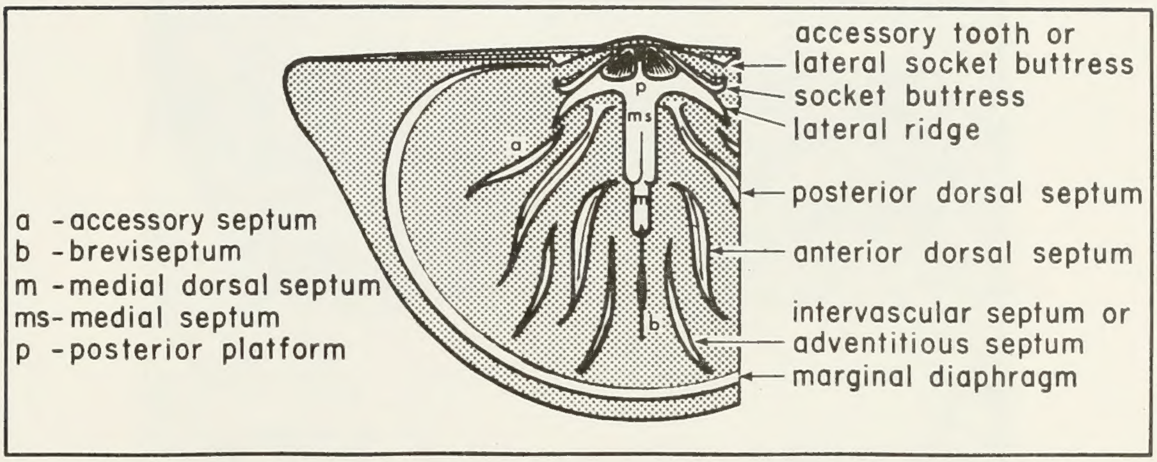
By convention, the "plane of commissure", Text-figure 1, D-a, is misused in this work and elsewhere with reference to the orientation of longitudinal and transverse sections of strongly curved concavo-convex and resupinate brachiopods. The line marked "plane of commissure" in Text-figure 1, D-a, is parallel to the plane which includes the line of commissure of a curved brachiopod as shown. It is customary to say that longitudinal sections are ground parallel to the plane of commissure and that transverse sections are ground normal to the plane of commissure. In reality, longitudinal sections are ground parallel to a plane tangential to the medial-posterior region of the external surface of the disk of the valve (see glossary for "disk of the valve") and transverse sections are ground normal to longitudinal sections. These orientations provide the most intelligible sections through structures of the internal surfaces of the valves.

## GENERAL MORPHOLOGICAL TERMINOLOGY OF STROPHOMENACEAN VALVES

The general morphological terminology of brachiopods is well known and does not need discussion here. Some of the general and specialized terms required for taxonomic description and discussion of the comparative morphology of the Strophomenacea are illustrated in Text-figures 2 through 6. The many standard and commonly used terms which appear in this work and which are satisfactorily defined in the glossary of the *Treatise on Invertebrate Paleontology, Part H, Brachiopoda* (pp. 138-155) do not require redefinition. The authors of the *Treatise* apparently believe that their glossary is complete. They stated (p. H3) that they hoped to have achieved ". . . a consistent terminology of manageable proportions that will act as a deterrent to any further maintenance of elaborate private vocabularies". Notwithstanding, detailed investigation of any group of organisms, fossil or living, is certain to uncover features and concepts which have not been recognized previously. New terms are necessary for these features and concepts to avoid awkward descriptive phrases and to avoid unfortunate implication of homology where none exists. Consequently, it has been necessary to assemble a "private vocabulary" of terms which are necessary for



*Text-figure 2.*—Morphological terms applicable to strophomenoid brachiopods. ca — cardinal angle, cp — cardinal process, dv — dorsal valve, gm — genital markings, vsa — *vascula arcuata,* vsb — *vascula bifurcata,* vsg — *vascula genitalia,* vsm — *vascula media,* vst — *vascula terminalia,* vsy — *vascula myaria,* vv — ventral valve. 1. The shape of the profiles of some brachiopods. The dorsal valve is directed toward the top of the page. 2. The shape of the geniculation of some brachiopods as seen in profile. Note that geniculation of the ventral valve results in geniculation in the dorsal direction, *i.e.* dorsal geniculation. 3. The shape of the anterior margin of some brachiopods. 4. A profile view of the anterior diaphragm of the dorsal valve, as found in species of *Murinella.* 5. A sharply geniculated flap or tongue on the anterior-medial margin of the ventral valve of *Notoleptaena* and *Rugoleptaena* fits against a complementary tongue of the dorsal valve. 6. The shape of brachiopod valves in plan-view. 7. Variation of the shape of the alae or cardinal angles of brachiopods. 8. Vascular markings on the internal surfaces of resupinate strophomenacean brachiopods. The vascular markings are reconstructed from traces on valves of several species of *Strophomena.* The ventral valve is on the left; the dorsal valve is on the right. 9. Vascular markings on the internal surfaces of concavo-convex strophomenacean brachiopods. A ventral valve is shown on the left, a dorsal valve on the right. The ventral valve (left) is reconstructed from several specimens of *Macrocoelia expansa,* see Text-figure 6, number 13. The dorsal valve (right) is reconstructed from published illustrations and several specimens of species of *Leptaena* and *Kiaeromena.*

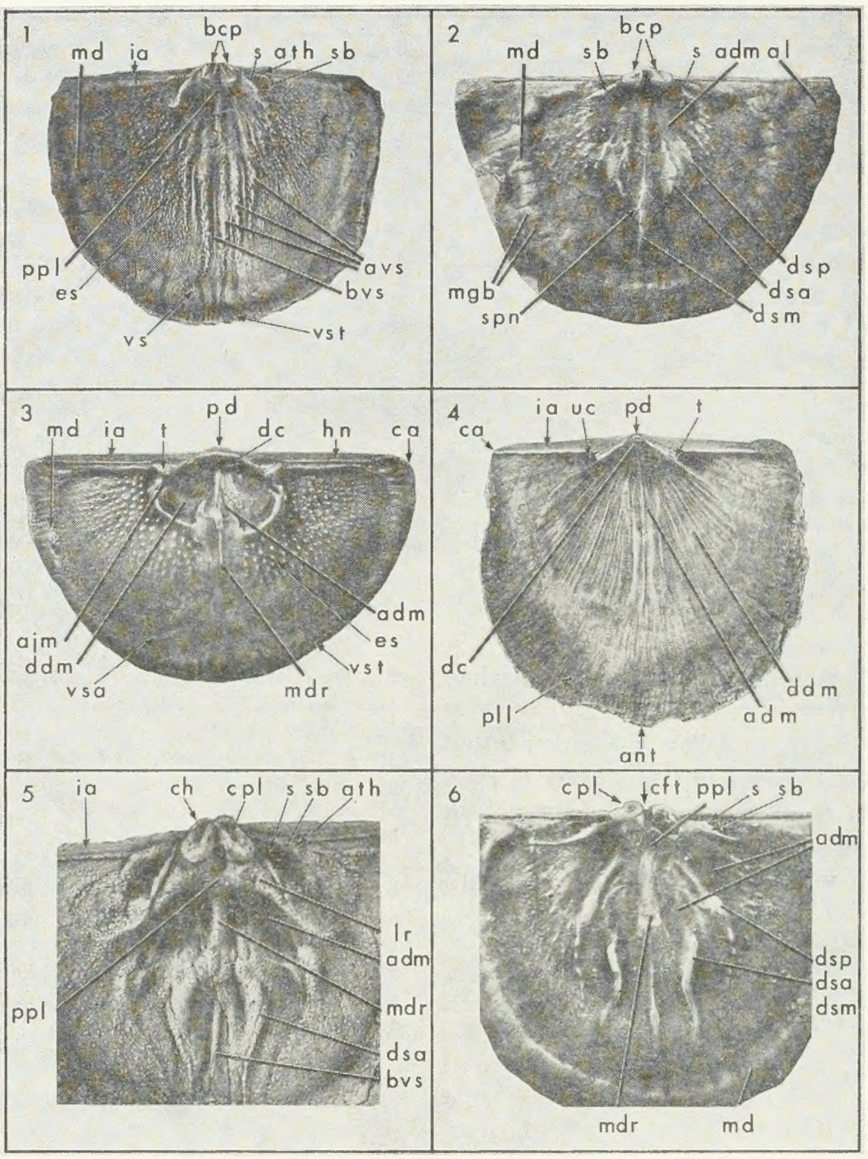


*Text-figure 3.*—The ridges on the internal surface of the dorsal valve of a generalized strophomenacean brachiopod. These structures may be called either ridges or septa depending upon their shape in various species. The lateral socket buttress may be called an accessory tooth if this structure has an articulatory function. The lateral ridge and medial septum or ridge are parts of the posterior platform. Intervascular septa may be called adventitious septa if their form is irregular. The accessory septa are intervascular septa which are not to be related to the five transmuscle dorsal septa. The medial dorsal septum is the medial member of the five transmuscle dorsal septa (i.e., it is a breviseptum overlain by secondary deposits) whereas the medial septum is the anterior projection of the posterior platform.

taxonomic description and morphological discussion of the Strophomenacea.

All entries in the glossary to follow are either new terms, rarely used terms not included in the glossary of the *Treatise,* terms defined in an unconventional manner for specific application to strophomenaceans, or terms of disputed definition for which a preferred definition has been selected.

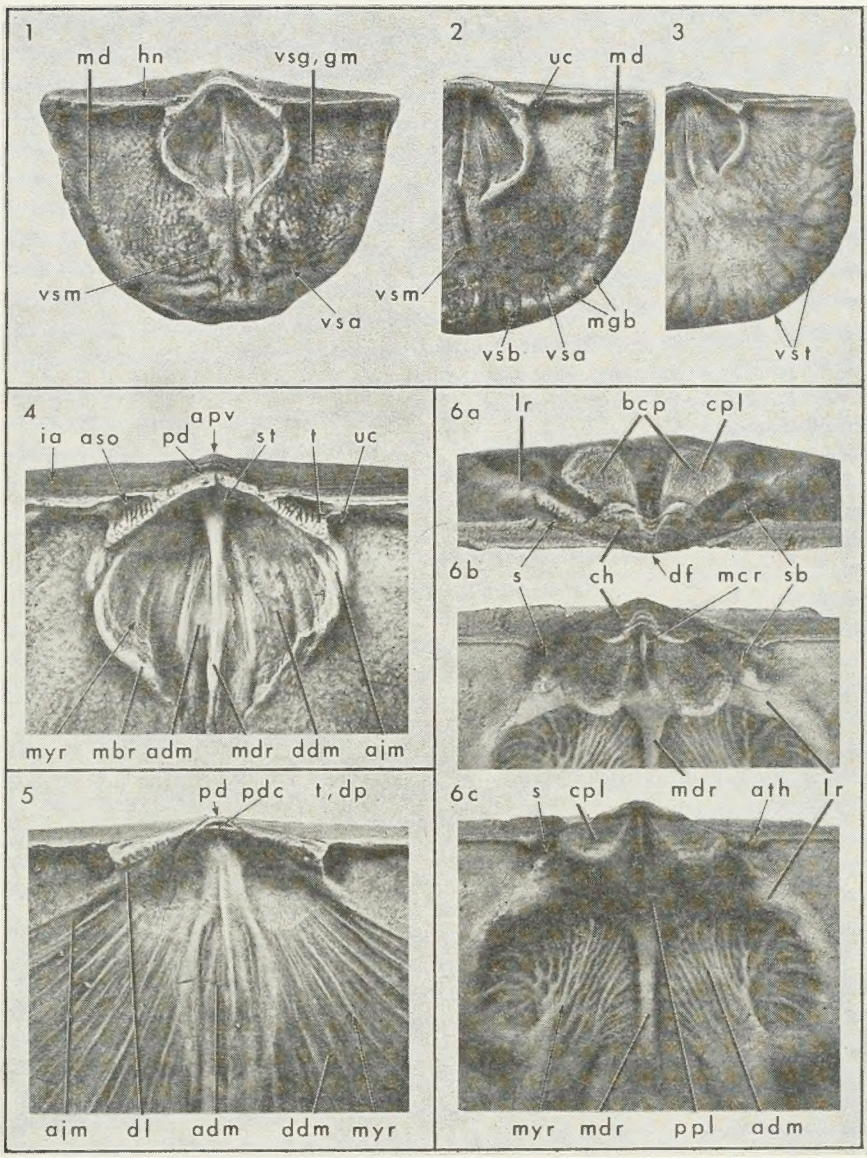
*Key to abbreviations on Text-figures 4, 5, and 6.*—
adm, adductor muscle scars. Fig. 4: 2,3,4,5,6; fig. 5: 4,5,6a.
ajm, adjustor muscle scars. Fig. 4: 3; fig. 5: 4,5.
al, ala. Fig. 3: 2; fig. 6: 14.
anm, anterior margin. Fig. 6: 14.
ant, anterior. Fig. 4: 4.
apv, apex of the valve. Fig. 5: 4; fig. 6: 14.
aso, accessory socket. Fig. 5: 4.
ath, accessory tooth. Fig. 4: 1,5; fig. 5: 6c.
avs, adventitious septa. Fig. 4: 1.
bcp, bifid cardinal process. Fig. 4: 1,2; fig. 5: 6a.
br, beak ridge. Fig. 6: 11.
bvs, breviseptum. Fig. 4: 1,5.
ca, cardinal angle. Fig. 4: 3,4.
cft, cleft. Fig. 4: 6.
ch, chilidium. Fig. 4: 5; fig. 5: 6a,6b; fig. 6: 11,12.
cpl, cardinal process lobe. Fig. 4: 5,6; fig. 5: 6a,6c.
dc, delthyrial cavity. Fig. 4: 3,4.
ddm, diductor muscle scar. Fig. 4: 3,4; fig. 5: 4,5; fig. 6: 13.
df, dorsal foramen. Fig. 5: 6a.
dkv, disk of the valve. Fig. 6: 14.
dl, dental lamella. Fig. 5: 5.
dn, dorsal node or protegular node. Fig. 6: 12.
dp, denticular plate. Fig. 5: 5; fig. 6: 8,11.
dsa, anterior dorsal septum. Fig. 4: 2,5,6.
dsm, medial dorsal septum. Fig. 4: 2,6.
dsp, posterior dorsal septum. Fig. 4: 2,6.
es, endospines. Fig. 4: 1,3.
fln, flange. Fig. 6: 8.
gm, genital markings. Fig. 5: 1; fig. 6: 13.
gn, geniculation. Fig. 6: 14.
h, hemisyrinx. Fig. 6: 10.
hn, hinge nick. Fig. 4: 3; fig. 5: 1.
ia, interarea. Fig. 4: 1,3,4,5; fig. 5: 4; fig. 6: 11.
lr, lateral ridge. Fig. 4: 5; fig. 5: 6a,6b,6c.
mbr, muscle bounding ridge. Fig. 5: 4; fig. 6: 10.
mcr, meso-cardinal ridge. Fig. 5: 6b.
md, marginal diaphragm. Fig. 4: 1,2,3,6; fig. 5: 1,2.
mdr, medial ridge. Fig. 4: 3,5,6; fig. 5: 4,6b,6c.
mgb, marginal beads. Fig. 4: 2; fig. 5: 2.
myr, myophore ridges. Fig. 5: 4,5,6c.
pc, pedicle conduit. Fig. 6: 10.
pd, pseudodeltidium. Fig. 4: 3,4; fig. 5: 4,5; fig. 6: 11,12.
pdc, pedicle callist. Fig. 5: 5; fig. 6: 9.
pll, papillae. Fig. 4: 4.
ppl, posterior platform. Fig. 4: 1,5,6; fig. 5: 6c.
prc, primary costa. Fig. 6: 1,4.
psm, posterior margin. Fig. 6: 14.
rg, ruga. Fig. 6: 6,14.
s, socket. Fig. 4: 1,2,5,6: fig. 5: 6a,6b,6c.
sb, socket buttress. Fig. 4: 1,2,5,6; fig. 5: 6a,6b.
scs, secondary costa. Fig. 6: 1,4.
spn, septa node. Fig. 4: 2.
st, spondylium triplex. Fig. 5: 4; fig. 6: 10.
t, tooth. Fig. 4: 3,4; fig. 5: 4,5; fig. 6: 8,9.
tr, trail. Fig. 6: 14.
uc, umbonal cavity. Fig. 4: 4; fig. 5: 2,4.
vs, vascular markings. Fig. 4: 1.
vsa, *vascula arcuata.* Fig. 4: 3; fig. 5: 1,2.
vsb, *vascula bifurcata.* Fig. 5: 2; fig. 6: 13.
vsg, *vascula genitalia.* Fig. 5: 1.
vsm, *vascula media.* Fig. 5: 1; fig. 6: 13.
vst, *vascula terminalia.* Fig. 4: 1,3; fig. 5: 3; fig. 6: 13.



*Text-figure 4*

1. *Strophomena vetusta* (James). Interior of dorsal valve. Whitewater Formation. Shideler locality 1.3C3, tributary of Paint Creek upstream from Devil's Backbone, about one mile west of Camden, Ohio, along Rt. 725. M.U. 130-T. Magnification about ×1.2.
2. *Oepikina septata* Salmon. Interior of dorsal valve. Lebanon Formation. U.S. Highway 70N, opposite Fairview Service Station, ½ mile west of Rome, Smith Co., Tennessee. Hypotype, U.S.N.M. 117830. Magnification about ×2.1.
3. *Strophomena planumbona elongata* (James). Interior of ventral valve. Clarksville Member, Waynesville Formation. Shideler locality 1.43A7, Penquite Hollow near Clarksville, Ohio. M.U. 131-T. Magnification about ×2.0.
4. *Rafinesquina ponderosa* Ulrich. Interior of ventral valve. Ft. Ancient Member of Waynesville Formation. Corner of Boudinot Avenue and Westwood-Northern Boulevard, Cincinnati, Ohio. M.U. 132-T. Magnification about ×1.02.
5. *Holtedahlina sulcata* (Verneuil). Posterior-central region of interior of dorsal valve of gerontic specimen. Probably Whitewater Formation. Shideler locality 2.1M, Richmond, Indiana, along road going up hill just across river (Whitewater River) from the Garr-Scott (Manufacturing) plant. M.U. 133-T. Magnification about ×3.4.
6. *Oepikina formosa* Cooper. Interior of dorsal valve. Pooleville Member of Bromide Formation. Rock Crossing of Hickory Creek, Carter Co., Oklahoma. Paratype, U.S.N.M. 117808 (figured, Cooper, 1956, pl. 243, 24-26, note right cardinal process lobe is missing). Magnification about ×2.9.

Abbreviations of morphological terms appear in the glossary.



*Text-figure 5*

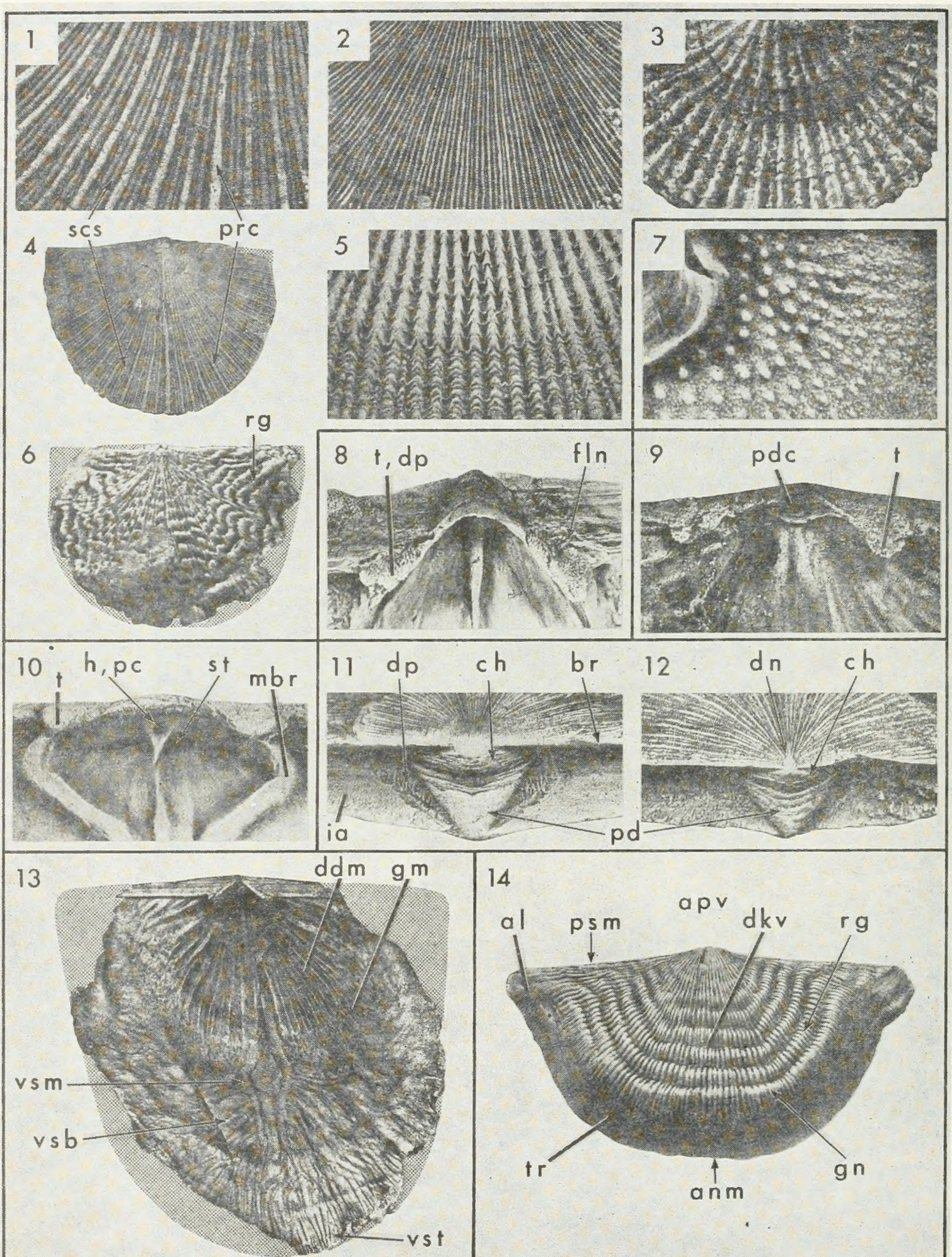
1-3. *Strophomena planumbona* (Hall). Interior of ventral valve of three individuals to show vascular sinuses. (1) Liberty Formation. Shideler locality 1.1S, exposures north of Mixerville Pike, just east of Indian Creek, Butler Co., Ohio. M.U. 134-T. Magnification about ×1.9. (2) Probably Liberty Formation, Oxford, Ohio area, M.U. 135-T. Magnification about ×2.0. (3) Probably Liberty Formation, Oxford, Ohio, area. M.U. 136-T. Magnification about ×2.0.

4. *Strophomena vetusta* (James). Posterior-central region of interior of ventral valve. Blanchester Member, Waynesville Formation. Schideler locality 1.1I7a, Collins Run (also called Bull Run) about ½ mile south of Oxford, Ohio, just upstream from railroad bridge, behind city dump. M.U. 137-T. Magnification about ×2.75.

5. *Rafinesquina ponderosa* Ulrich. Posterior-central region of interior of ventral valve. Same specimen as shown in Figure 4, 4. M.U. 132-T. Magnification about ×2.7.

6. *Rafinesquina ponderosa* Ulrich. Three views of posterior-central region of the interior of the dorsal valve. Arnheim Formation. Shideler locality 1.1J2, Martindells Creek, first tributary to Four Mile Creek south of valley of Collins Run, Butler Co., Ohio. M.U. 138-T. Magnification about ×2.9. (6a) View parallel to commissure. (6b) Specimen rotated about 60 degrees from horizontal. (6c) View normal to commissure.

Abbreviations of morphological terms appear in the glossary.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*Text-figure 6*

1. *Rafinesquina fracta* ? (Meek). Prosopon on external surface of ventral valve. Blanchester Member, Waynesville Formation. Shideler locality 1.117a, Collins Run (also called Bull Run) about ½ mile south of Oxford, Ohio, just upstream from railroad bridge, behind city dump. M.U. 139-T. Magnification about ×4.4.
2. *Strophomena planumbona subtenta* (Hall). Prosopon on external surface of dorsal valve. Formation and locality unknown. Charles Dyche collection at Miami University. M.U. 140-T. Magnification about ×5.0.
3. Gen. and sp. indet. Scoticoid prosopon on external surface of ventral valve. Beech River Formation (Silurian). Glade just south of Mt. Lebanon School, Perryville Quadrangle, Tennessee. U.S.N.M. 174688. Magnification ×3.9. Prosopon resembles that of *Strophomena* [?] *scotica* Bancroft.
4. *Kjaerina squamula* (James). Exterior of ventral valve. Southgate Member, Latonia Formation. Large excavation behind Newport Shopping Center, Rt. 27, Newport, Kentucky. M.U. 141-T. Magnification about ×3.3.
5. *Glyptorthis insculpta* (Hall). Prosopon on exterior of ventral valve. Blanchester Member, Waynesville Formation. Shideler locality 1.1B2, Addison's Creek, 3 miles north of Oxford, Ohio. M.U. 142-T. Magnification about ×5.5. For comparison to previous illustrations.
6. *Bellimurina subquadrata* Cooper. Exterior of dorsal valve. Mountain Lake Member, Bromide Formation. Three miles northeast of Springer, Carter Co., Oklahoma. Paratype, U.S.N.M. 117655c. Magnification about ×5.4.
7. *Strophomena planumbona elongata* (James). Magnified view of region on interior of ventral valve, just to right of muscle area. Same specimen as shown in Figure 2, 3. M.U. 131-T. Magnification about ×7.8.
8. *Strophomena vetusta* (James). Posterior-central region of interior of ventral valve of gerontic individual. Formation and locality not known, except from the Oxford, Ohio, area. M.U. 143-T. Magnification about ×3.3.
9. *Macrocoelia expansa* (Sowerby). Latex cast of posterior-central region of interior of ventral valve. Caradoc Sandstone ($C_4$ of King, 1928), Soudleyan. Meiford District, Montgomeryshire, Wales, west side of Gallty Aner. U.S.N.M. 105890; latex cast, M.U. 144-T. Magnification about ×3.4.
10. *Strophomena planumbona* (Hall). Posterior-central region of interior of ventral valve; specimen tilted. Liberty Formation. Large roadcut on Rt. 127, about one mile south of Camden, Ohio. M.U. 145-T. Magnification about ×4.4.

11-12. *Strophomena planumbona subtenta* (Hall). Medial region of the interarea of two specimens. Specimens inclined for maximum view of pseudodeltidium and chilidium. Dorsal valve is up. Formation and locality unknown. Charles Dyche Collection at Miami University, number De280D on both specimens. (11) M.U. 146-T, (12) M.U. 147-T. Magnification about ×5.2.

13. *Macrocoelia expansa* (Sowerby). Latex cast of internal surface of ventral valve, valve outline reconstructed. Caradoc Sandstone ($C_4$ beds of King, 1928), Soudleyan. Allt Fawr, Meiford District, Montgomeryshire, Wales. U.S.N.M., no number, late cast M.U. 148-T Magnification about ×1.5.
14. *Leptaena richmondensis* (Foerste). External surface of ventral valve. Blanchester Member, Waynesville Formation. Shideler locality 1.117a, Collins Run (also called Bull Run) about ½ mile south of Oxford, Ohio, just upstream from railroad bridge, behind city dump. M.U. 149-T. Magnification about ×1.95.

Abbreviations of morphological terms appear in the glossary.

## GLOSSARY

*accessory septa.* See dorsal septa.

*accessory socket.* A shallow groove or pit in the palintrope of the ventral valve lateral to the denticular plate. The accessory socket accommodates the accessory tooth or lateral socket buttress of the dorsal valve.

*accessory tooth.* A ventrally directed projection from along the posterior-lateral margin of the socket of the dorsal valve (lateral socket buttress) which articulates with a groove or pit (accessory socket) lateral to the denticular plate in the palintrope of the ventral valve.

*adventitious septa* or *ridges.* Septa of the internal surface of the dorsal or ventral valve exclusive of the true dorsal septa, accessory septa and medial septum. Adventitious septa correspond to intervascular septa but adventitious septa have irregular form and commonly are not bilaterally arranged.

*alternate costae.* Costae which alternate large and small, that is, primary and secondary.

*anderidium (a).* The pair of septa or ridges which flank the medial septum or ridge on the internal surface of the dorsal valve of chonetoids and plectambonitoids. The anderidia of plectambonitoids possibly correspond to the anterior-dorsal ridges of the Strophomenacea.

*anterior diaphragm.* A high septum on the internal surface of the dorsal valve which is concentric to the anterior margin of the valve. The anterior diaphragm is a modification of the marginal diaphragm in the anterior region. The anterior diaphragm bridges the space between the two valves and may cause a complementary groove in the ventral valve. The anterior diaphragm is most pronounced in species of ***Murinella.***

*anterior dorsal septa* or *ridges.* See dorsal septa.

*apex of the valve.* The posterior-most point of a brachiopod valve where the protegulum is situated. Radially disposed features of brachiopods, *e.g.* costae, converge toward the apex of the valves. Strophomenaceans do not have elongated "beaks" as have other groups of brachiopods. The apex of the valve has been called the "umbo" but authors have used umbo with conflicting meanings.

*bimuroid prosopon.* External aspect caused by the anterior extension of the edges of coarse varices (comae) at regular intervals along the length of the valve. The comae commonly are deformed and chipped and impart a rough and ragged appearance to the valve. The bimuroid aspect is well developed on the dorsal valve of *Bimuria buttsi* Cooper.

*brachial ridges.* A synonym of dorsal ridges.

*breviseptum.* A thin septum which extends anteriorly from the anterior end of the medial ridge of the posterior platform of the dorsal valve. The breviseptum of strophomenaceans appears to correspond to the breviseptum of chonetoids and productoids. The breviseptum is composed of coarsely granular calcite in contrast to the lamellar calcite of adjacent shell tissue.

*cancellus tissue.* A microstructural type of shell tissue which has a cellular character. In the Strophomenacea, the cancellus structure seems to be confined to the muscle attachment sites on the cardinal process lobes.

*cardinal process.* A process or processes which project inward from the internal, medial-posterior surface of the dorsal valve and which serve for attachment of the diductor muscles. The cardinal process of the Strophomenacea is bifid, that is, divided into two lobes. Descriptive terms applied to cardinal process lobes are: blade (tabular, elongated in anterior-posterior direction), shaft (short, cylindrical, erect), cylindrical (tall, erect, round in cross section), lobate (irregular, short, obese), petaloid (top flattened and overhanging, as a mushroom, flattened top generally wider at anterior end than posterior end), hooked (ventral end curved in posterior direction).

*cardinal process lobe.* One process of the pair of processes which together constitute the bifid cardinal process of the Strophomenacea.

*chilidium.* By conventional definition, the flat or convex plate which partly or completely closes the notothyrium. The dorsal interarea of strophomenaceans is so narrow that a posterior-medial notch, the notothyrium, is obscure. For the Strophomenacea, the chilidium must be defined as continuation of the microcrystalline tissue of the interarea which extends from socket to socket across the posterior faces of the cardinal process lobes. The chilidium covers that part of the posterior base of the cardinal process which would be exposed by the delthyrium. No evidence of paired chilidial plates occurs in the Strophomenacea.

*christianioid prosopon.* The external aspect of a valve which is smooth. The surface of the valves of most species of ***Christiania*** bear, at most, only the faintest traces of capillae and fila.

*clear lamellar tissue.* A type of secondary deposit which is lamellar and which is brighter or clearer than other lamellar tissue when observed in peel sections.

*cleft.* The space between the lobes of a bifid cardinal process.

*compound prosopon pattern.* The external surface of valves of some species may bear two superimposed prosopon patterns. This condition is called a compound pattern. Prosopon patterns are listed under "prosopon".

*conjunct cardinal process.* A type of bifid cardinal process in which the posterior ends of the lobes are pressed together or ankylosed. The posterior ends of conjunct cardinal process lobes are covered commonly by the chilidium.

*cupped myophore.* A myophore surface on a cardinal process lobe that is cupped or folded.

*cymostrophioid prosopon.* A type of external prosopon in which the valve has the appearance of seersucker fabric. The surface of the valve bears widely spaced primary costae separated by fields of secondary costae. Each field between primary costae is rugose. The rugae of adjacent fields are alternate, that is, an outward projecting ruga lies next to an inward projecting ruga. The alternating rugae of many species are not so regular as to produce a definite geometric pattern. The rugae of a few species do form geometric patterns resembling a checkerboard made of rhombs. The cymostrophioid aspect is named for the stropheodontid genus *Cymostrophia.*

*dark lamellar tissue.* A type of secondary deposit which is lamellar and which is darker than other lamellar tissue when observed in peel sections.

*dental lamella (ae).* Tabular, vertical structures which unite the teeth and delthyrial margin of the palintrope of the ventral valve with the posterior-internal surface of the ventral valve. The tissue of the dental lamellae is confluent with the tissue of the palintrope and the internal surface of the valve, that is, dental lamellae are not bounded by sutures. Structures with similar position which are sutured to the floor of the valve and to the palintrope should be called dental plates. Dental plates are not found in the Strophomenacea.

*denticular plate.* A plate in the tooth of strophomenoid brachiopods which is sutured along the ventral edge or surface to the dental lamella and along the lateral surface to the palintrope. The denticular plate is the principal articulatory projection. The denticular plate is composed of lamellar tissue formed into tabular pseudopunctae in the Strophomenacea.

*dictyostrophioid prosopon.* An external prosopon pattern formed by the crossing of varices and secondary costae of equal prominence. Stronger primary costae divide the reticulate pattern into fields. The compound pattern resembles the surface of some fossil hyalosponges, *e.g. Dictyospongia.* The pattern is named for the stropheodontid brachiopod *Dictyostrophia.*

*disjunct cardinal process.* A type of bifid cardinal process in which the lobes are distinctly separated.

*disk of the valve.* A valve minus the palintrope.

*dorsal foramen.* The dorsal foramen is a questionable perforation near the apex of the dorsal valve of juvenile strophomenaceans. Thin sections through the apex of the dorsal valve of adult strophomenaceans show a point of very thin shell at the apex of the notothyrial cavity and the posterior edge (juvenile edge) of the chilidium. This thin spot in the shell separates the bulbous base of the chilidium from the long, thin plate of the adult chilidium. Probably the dorsal foramen is always closed by secondary deposits in adult strophomenaceans. Rupture of the thin filling of secondary tissue may give rise to an apparent dorsal foramen in adults at the site of the original dorsal foramen (Text-figure

5, 6a). The function of the dorsal foramen is not definitely established. Spjeldnaes (1957) suggested that the dorsal foramen may be a juvenile pedicle foramen.

*dorsal geniculation.* Dorsal geniculation refers to an angular bend in the valves, concentric to the margin, such that the trail is flexed in the dorsal direction.

*dorsal node.* A node or facette on the apex of the dorsal valve. According to Kemežys (1965, p. 505) the dorsal node of Spjeldnaes (1957, pp. 50-52) is equivalent to the dorsal protegular fold. The dorsal node is also called the protegular node.

*dorsal septa* or *ridges.* A set of five ridges or septa which are found on the internal surface of the dorsal valve of many species of strophomenaceans. The five ridges include the medial dorsal septum, a pair of anterior dorsal septa and a pair of posterior dorsal septa. The medial dorsal septum may be the breviseptum or may be a breviseptum covered by secondary shell deposits. The medial dorsal septum is a projection of the medial ridge of the posterior platform anterior to the adductor muscle scars. The medial ridge of the posterior platform commonly is wider than the medial dorsal septum because of addition of secondary tissue along the medial borders of the muscle scars. The anterior dorsal septa may correspond to the anderidia of the plectambonitaceans. The posterior dorsal septa arise in the boundary between the anterior and posterior adductor muscle scars.

Synonyms for the dorsal septa include transmuscle septa and brachial septa. Synonyms for the anterior and posterior pairs of dorsal septa include anterior and posterior lateral septa, floor plates, standing plates and submedian septa.

Other septa or ridges may be found on the interior of the dorsal valve which may be confused with the true dorsal septa. These are the intervascular septa or ridges which border or overlie the vascular channels in the shell. Adventitious septa are irregularly formed intervascular septa. The pair of accessory septa may lie between the posterior dorsal septa and the lateral ridges of the posterior platform. The accessory septa may resemble the true dorsal septa but the accessory septa are intervascular (*i.e.* adjacent to the *vasculae cruralia*).

*drape.* The fold of the chilidium into the cleft of the bifid cardinal process.

*endospines.* Short, sharp, elevated spines on the internal surface of either valve. An endospine generally encases the end of a taleola. There is little difference between endospines and papillae except that endospines are sharp and erect and papillae are blunt, lobate or pimple-like and very short or recumbent.

*flange.* The flange is a structure encased entirely within the shell material of the ventral palintrope. The flange has no expression on either the external or internal surface of the palintrope or valve. The flange is a ridge on the ventral surface (underside) of the microcrystalline layer of the ventral palintrope which projects between the lateral surface of the denticular plate and lamellar tissue at the junction of the dental lamella and the palintrope. See Text-figure 6, number 8, and Text-figure 25.

*floor plates.* Synonym for the anterior and posterior dorsal septa.

*fulcral plates.* Concave plates of lamellar tissue which constitute the lateral part of the socket plates. The fulcral plates line the inner surface of the socket of the Strophomenacea and brace the socket buttress. Accessory teeth seem to be formed from the fulcral plates. The fulcral plates of Strophomenacea should be called "recumbent fulcral plates" because they are fused into the floor of the socket.

*glyptomenoid prosopon.* The external prosopon pattern shown by *Glyptomena* in which there are wide fields of uniform secondary costellae separated by primary costae.

*granular tissue.* See microcrystalline tissue.

*hinge nick.* A groove on the interarea parallel and near to the free, anterior edge of the palintrope. The hinge nick may mark the site of attachment of a ligament or the site of abrasion by the edge of the opposing interarea.

*initial layers.* — The layers of the brachiopod shell which are secreted at the margin of the mantle. These include the periostracum, outer carbonate layer and inner initial layer. The boundary of the initial layers and the secondary deposits is indistinct.

*inner initial layer.* — The mineral shell layer which underlies the outer carbonate layer. The inner initial layer is secreted by the margin of the mantle. In the Strophomenacea, the inner initial layer is lamellar and pseudopunctate. For synonyms, see Table 2.

*intervascular septa.* — Septa situated between or upon the main branches of the vascular channels in the shell. Intervascular septa which are irregular in form are called adventitious septa.

*kjaerinoid costa.* — One exceptionally prominent costa along the midline of the valve, usually the ventral valve. This common feature is prominently displayed by species of the genera *Kjaerina, Megamyonia* and *Kjerulfina.*

*lateral.* — The direction opposite to medial, that is, toward the sides of the valve.

*lateral ridge.* — The ridge which extends laterally from the base of the cardinal process or from the posterior end of the medial ridge of the dorsal valve. The lateral ridges form the blades of the anchor-shaped posterior platform. The posterior margin of the lateral ridges may merge with the socket buttresses. The lateral ends of the lateral ridges may merge with the posterior-medial ends of the marginal diaphragm. The adductor muscle scars lie in the crotches between the lateral ridges and the medial ridge. "Lateral ridge" as defined corresponds to the lateral ridge of productoids as used by Muir-Wood and Cooper (1960) but not to "lateral septa" (=anderidia) of chonetoids as used by Muir-Wood (1962).

*leptaenoid prosopon.* The external pattern of prosopon in which uniform or alternate costae are crossed by regularly spaced concentric rugae, as shown on species of *Leptaena* and *Kiaeromena.*

*marginal beads.* Rounded nodes along the course of the marginal diaphragm. The marginal beads are commonly best developed near the anterior-medial margin of the dorsal valve. Marginal beads are formed by interruption of the marginal diaphragm by vascular canals.

*marginal chamber* or *marginal tunnel.* A tunnel or chamber around the lateral and anterior margins of articulated valves between the marginal diaphragms of both valves and the edges of the valves. The *vascula terminalia* are found on the surface of the marginal chamber.

*marginal diaphragm.* A low ridge on the internal surface of a valve which is concentric to the margin of the valve. The marginal diaphragm arises in the umbonal cavity or at the lateral ends of the lateral ridges. The marginal diaphragm may be interrupted in the medial-anterior region for passage of the *vascula media.* The marginal diaphragm separates the surface of the visceral cavity from the surface of the marginal chamber upon which are found the channels of the *vascula terminalia.* The marginal diaphragm may be a low ridge or a high septum as in species of *Murinella.* Marginal diaphragm of the strophomenacea is equivalent to the marginal ridge of the Productoidea.

*medial.* The posterior to anterior line or plane which divides the valve (or articulated valves) into equal, mirror-image halves. Also used to mean toward the medial line or plane. The direction opposite to medial is "lateral".

*medial ridge.* The medial-anterior projection of the posterior platform of the dorsal valve or a medial ridge which separates the diductor and adductor muscle scars of the ventral valve.

*meso-cardinal ridge.* A ridge or septum in the cleft between the lobes of a bifid cardinal process. Also called the "undifferentiated process".

*microcrystalline tissue.* Microscopically granular shell tissue associated with the surface of the palintrope or with muscle scars. This is the fibrous tissue of authors. In strophomenoids the crystalloid units of this tissue tend to be more equidimensional than elongated.

*myophore ridges.* The low ridges on muscle scar areas. The myophore ridges usually are radially oriented. They are most pronounced on the diductor muscle scars.

*nervose prosopon.* The external prosopon pattern found on *Nervostrophia* in which the primary costae, and to a lesser extent, the secondary costae, vary in height along their length from apex to margin. The interruptions of the costae are random in position and impart to the surface a rough appearance.

*notothyrial platform.* In strophomenoid brachiopods the notothyrial platform is called the posterior platform. Notothyrial platform should not be used in reference to strophomenoids because the posterior platform is not situated near the notothyrium. A notothyrial cavity may be designated in strophomenoids as the space beween the chilidium and the posterior surface of the bases of the cardinal process lobes.

*outer carbonate tissue.* The thin, external layer of mineral shell tissue in brachiopods. The outer carbonate layer underlies the periostracum. The outer carbonate layer on the disk of the valves of the Strophomenacea is finely lamellar; the layer may be finely granular in other brachiopod groups. For synonyms, see Table 2.

*palintrope.* The posterior, flexed part of a brachiopod valve. The external surface of the palintrope is the interarea. Palintrope is here defined in the sense of Thomson (1927, p. 47, not p. 64), Shrock and Twenhofel (1953, p. 293), Moore, Lalicker and Fischer (1952, p. 210) and Schuchert and Cooper (1932, p. 9). Cloud's definition of palintrope (1942, p. 14) which is based upon Thomson's definition (1927, p. 64, not pp. 49-50 which Cloud cited) restricts palintrope to a synonym of false cardinal area. Cloud's definition must be rejected by convention and because Cloud's definition leaves the prominent and important reflexed part of the valve without a suitable name.

*papillae.* Short or recumbent, blunt, lobate, or pimplelike projections on the internal surface of either valve. Papillae may or may not encase taleolae.

*pedicle conduit.* The conduit within the shell material of the apex of the ventral valve which served for protrusion of the pedicle. The external expression of the pedicle conduit is the pedicle foramen.

*pedicle tube* or *sheath.* A tube on the external, medial-posterior surface of the ventral valve of juvenile strophomenoid brachiopods through which the pedicle extended.

*plate.* A discrete structure joined to the rest of the shell by sutures. The tissue of a plate is not confluent with the tissue of the rest of the valve. The only plates of Strophomenacea are the socket plates and the denticular plates. "Dental plate" is inappropriate in reference to the Strophomenaca.

*posterior-dorsal septa* or *ridges.* See dorsal septa.

*posterior platform.* An anchor-shaped thickening in the medial-posterior region of the dorsal valve from which arises the cardinal process. The posterior platform is composed of the medial septum and the lateral ridges. "Posterior platform", Muir-Wood and Cooper (1960, p. 7), replaces "notothyrial platform" in reference to strophomenoids because the platform is not located under the notothyrium and because the platform may extend a considerable distance anterior to the base of the cardinal process.

*posterior rugae.* Localized rugae near the posterior margin and cardinal extremities of brachiopod valves. The posterior rugae commonly are oblique, that is, not concentric to varices and fila.

*prosopon.* Prosopon signifies those generally repetitive surface features of fossils which are judged to have minor taxonomic importance. Among brachiopods, prosopon includes features as costae, rugae and papillae. Prosopon replaces the term "ornament" because prosopon carries no asthetic connotation.

Different patterns and combinations of prosopon on the external surfaces of brachiopods may be named for genera or species which typically carry the pattern. For strophomenaceans, it is convenient to recognize the following patterns: bimuroid, christianioid, cymostrophioid, dictyostrophioid, glyptomenoid, nervose, leptaenoid, ptychoglyptoid, rafinesquinoid, scoticoid, sowerbyelloid and strophomenoid. These patterns are indexed separately in this glossary.

*protegular fold.* A medial node or fold on the dorsal protegulum of strophomenide brachiopods. Equivalent to the dorsal node.

*pseudodeltidium.* A flat to convex structure of the ventral valve which extends across part of the delthyrium between the medial-dorsal edges of the dental lamellae. The pseudodeltidium is confluent with the microcrystalline tissue on the surface of the palintrope; the pseudodeltidium does not possess a medial suture. The microcrystalline tissue of the pseudodeltidium may have a backing of secondary tissue. Pseudodeltidium is used in preference to "deltidium" of Shrock and Twenhofel (1953, p. 285) and "xenidium" of Cloud (1942, p. 20).

*ptychoglyptoid prosopon.* — The external prosopon pattern exhibited by *Ptychoglyptus* and *Bellimurina* in which rugae between adjacent or nearly adjacent primary costa are chevron-shaped, with the apex of each chevron pointed toward the apex of the valve.

*rafinesquinoid prosopon.* — The common prosopon pattern, as found on *Rafinesquina,* which is composed of primary costae which separate narrow fields of secondary and tertiary costae. The rafinesquinoid pattern differs from the glyptomenoid pattern in the narrowness of the fields between the primary costae and differentiation of costae therein.

*scoticoid prosopon.* — External prosopon in which the intersection of each major costa and varix is accentuated by a node. Commonly, the node is comma-shaped, with the tail of the comma lying along the varix. The tails of the commas may point alternately to either side along the length of a costa. This alternation gives the costa a zig-zag appearance. This aspect is named for *Strophomena scotica* Bancroft; this pattern is well developed also on *S. scabrosa* (Davidson).

*secondary deposits.* Mineral shell tissue deposited on the internal surface of the inner initial layer posterior to the margin of the mantle. Secondary deposits in the Strophomenacea are composed of lamellar or granular tissue and are rarely taleolate or pseudopunctate. For synonyms, see Table 2.

*semidenticles.* The irregular denticles on the dorsal and medial surfaces of the denticular plate of strophomenaceans.

*septal nodes* or *septal bosses.* Elevated nodes near the anterior ends of the dorsal septa.

*shaft buttresses.* Vertical lamellae which are oriented parallel to the medial sagittal plane and which buttress the anterior bases of the cardinal process lobes.

*size.* Species of Strophomenacea are described arbitrarily according to the following size classes for adults: small, specimens generally less than 20 mm (3/4 in.) wide; medium, specimens generally between 20 mm and 40 mm (1½ in.) wide; large, specimens generally larger than 40 mm wide.

*socket buttress.* A ridge which extends along the medial margin of the socket. The socket buttress contains the granular blade or rod of the socket plate. "Socket buttress" is preferred to "socket ridge" because socket ridge has been used for structures of several brachiopod groups which are not closely related to strophomenoids. See Muir-Wood (1962, p. 21).

*socket ridge.* See socket buttress.

*socket plate.* A plate which lines the sockets of the Strophomenacea. The socket plate is formed of two pieces, a granular blade or rod located along the medial margin of the socket and a concave plate of dark, finely lamellar tissue in the base of the socket. The granular blade or rod may be homologous to the brachiophore of the orthoids, at least they have the same microstructure and position. The concave plate of dark lamellar tissue may be a homologue of the fulcral plate of orthoids. Williams (1953) called the socket buttress a socket plate.

*sowerbyelloid prosopon.* The pattern of prosopon found on species of *Sowerbyella* in which the secondary costae and, to a lesser extent, the primary costae are rows of tiny beads formed at the intersection of the costae and varices. The sowerbyelloid pattern resembles the scoticoid pattern except that the nodes of the scoticoid pattern occur only on primary costae, are large and tend to cause the costae to zig zag, whereas the beads of the sowerbyelloid pattern are small and uniformly distributed.

*standing plates.* Thin, high, anterior dorsal septa which partition the internal cavity between the valves into chambers. Standing plates may extend across the entire thickness of the internal cavity between the valves. The exaggerated standing plates of some specimens of *Teratelasma neumani* Cooper perforate the ventral valve.

*strophomenoid prosopon.* The common external pattern of prosopon exhibited by many species of *Strophomena,* in which fine, uniform costae are crossed by faint varices.

*tongue.* A flap of shell at the anterior-medial margin of a valve which bears a sulcus. The tongue fits into the complementary space provided by the fold along the anterior-medial margin of the opposing valve.

*uniform costa.* Costae of regular size which cannot be divided into primary and secondary ranks by reference to size.

*varix (varices).* A growth line. Minor varices, fila, are the fine, regularly spaced concentric lines on the external surfaces of valves. Major varices are the coarse, randomly spaced concentric grooves on the external surface of a valve which are evidence of a major interruption of growth.

*vascular canals, channels* or *markings.* Branching canals produced by the impression of vascular sinuses (=pallial sinuses) upon the internal surfaces of valves. "Vascular sinuses" or "pallial sinuses" properly refer to elongated cavities within the flesh of the brachiopod and consequently should not be applied to the marks which they produce in the shell.

*ventral geniculation.* Geniculation of the valves such that the trail is bent in the ventral direction. This is opposite to dorsal geniculation in which the trail is bent in the dorsal direction.

*visceral cavity.* The central-medial region of the internal surface of the valves to which was attached the visceral mass of the living animal including the muscles.

*visceral disk.* The portion of the disk of the valve which overlies the visceral cavity on the internal surface of the valve upon which was situated the principal organs and muscle attachment areas of the living animal.

## SYSTEMATIC PALEONTOLOGY

The principal aim of this work is to document the comparative morphology of selected features and the shell histology of the Ordovician Strophomenacea. In such work, it becomes necessary to refer to taxa, most generally of generic or familial rank. This systematic review of the Strophomenacea is presented to permit the cited genera and families to be placed in their proper context within the superfamily. The concept of the Superfamily Strophomenacea has had a long and complex history in paleontology. The evolution of the strophomenacean concept, from 1846 when King proposed the family Strophomenidae to Muir-Wood's and Cooper's comprehensive classification in 1960, is summarized in Chart 5, in the pocket at the end of this manuscript.

The recently published *Treatise on Invertebrate Paleontology, Part H* (1965) contains diagnoses of the families and genera, notation of the type species of genera, geographic and stratigraphic range of genera, and illustrations of the type species of genera of the Strophomenacea (pp. H383-H395). The familial assignments and diagnoses of some genera presented in the *Treatise* are not acceptable to this writer whose classification of the group was constructed by phylogenetic analysis prior to publication of the *Treatise.* The differences between the classifications of the *Treatise* and this manuscript are minor and should not be stressed. They are largely differences of opinion as to where familial boundaries should be constructed with respect to transitional genera and differences of opinion concerning the rank of suprageneric taxa. The writer was surprised and pleased to review the classification in the *Treatise* because the *Treatise* supported so many of the systematic conclusions concerning the Strophomenacea which has been independently derived, even to the creation of several identical suprageneric taxa names.

There is a movement in paleontology today to standardize the endings of suprageneric taxonomic names. The International Code of Zoological Nomenclature specifies endings for familial-rank taxa only. These endings are "ini" for tribe, "inae" for subfamily, "idae" for family and "acea" for superfamily. Standardized endings for suprafamilial taxa of brachiopods have been adopted in the *Treatise* although such endings are not required by the International Code. The standardized endings are "idina" for suborder and "ida" for order. It is convenient and conventional to modify suprageneric taxonomic names to form vernacular nouns and adjectives. A recommendation is made in Footnote 1 of the *Treatise,* p. H12, that the endings of vernacular nouns formed from proper taxonomic names be constructed as follows: "ins" from subfamily names, "ids" from family names, "aceans" from superfamily names, "idines" from suborder names and "ides" from order names. The adjectival form of each vernacular noun is constructed by deleting the final "s". Most of this manuscript was written before publication of the *Treatise.* The recommended endings have been adopted herein with the exception that the more conventional termination "oids" is employed for the vernacular form of subordinal taxa, *e.g.* the suborder Strophomenidina, the strophomenoids.

An outline of the suprageneric classification is given below to assist in the correlation of the present classification with that of the *Treatise on Invertebrate Paleontology, Part H, Brachiopoda* (1965). Illustrations of the type species of most genera of the Strophomenacea may be seen in the *Treatise* (pp. H383-H395). Additional illustrations of many species may be found in Cooper (1956, plates 208, 212-267) and Spjeldnaes (1957, plates 6-14).

A comparison of the strophomenacean classification of the Treatise and that employed in this study. —

Classification of the Treatise

Superfamily Strophomenacea King, 1846
- Family Strophomenidae King, 1846
    - Subfamily Strophomeninae King, 1846
    - Subfamily Furcitellinae Williams, 1965
    - Subfamily Rafinesquininae Schuchert, 1893
    - Subfamily Glyptomeninae Williams, 1965
    - Subfamily Oepikinae Sokolskaya, 1960
    - Subfamily Leptaenoideinae Williams, 1953
- Family Foliomenidae Williams, 1965
- Family Christianiidae Williams, 1953
- Family Leptaenidae Hall and Clarke, 1894
- Family Stropheodontidae Caster, 1939
    - Subfamily Stropheodontinae Caster, 1939
    - Subfamily Leptostrophiinae Caster, 1939
    - Subfamily Douvillininae Caster, 1939
    - Subfamily Pholidostrophiinae Stainbrook, 1943
    - Subfamily Shaleriinae Williams, 1965
    - Subfamily Leptodontellinae Williams, 1965
    - Subfamily Liljevalliinae Williams, 1953

Classification in this work

Superfamily Strophomenacea King, 1846
- Family Oepikinidae Sokolskaya, 1960
- Family Rafinesquinidae Schuchert, 1893
- Family Leptaenidae Hall and Clarke, 1894
    - Subfamily Murinellinae, new
    - Subfamily Leptaeninae Hall and Clarke, 1894
    - Subfamily Leptaenoideinae Williams, 1953
- Family Strophomenidae King, 1846
    - Subfamily Furcitellinae Williams, 1965
        - Tribe Furcitellini Williams, 1965
        - Tribe Glyptomenini Williams, 1965
        - Tribe Teratelasmini, new
    - Subfamily Strophomeninae King, 1846

Superfamily Christianiacea Williams, 1953

Superfamily Stropheodontacea Caster, 1939

## Phylum BRACHIOPODA Duméril, 1806

## Class ARTICULATA Huxley, 1869

## Order STROPHOMENIDA Öpik, 1934

## Suborder STROPHOMENIDINA Öpik, 1934

### Superfamily **STROPHOMENACEA** King, 1846

*Diagnosis.* — Pseudopunctate and generally taleolate, finely costate strophomenoids, with concavo-convex, resupinate, biconvex or rarely plano-convex profile, wide hinge line, relatively narrow interarea, bifid cardinal process and a supra-apical pedicle foramen.

*Description.* — In addition to the diagnostic features, all strophomenaceans bear a pseudodeltidium and chilidium. The pseudodeltidium or chilidium may be reduced in certain species with complementary enlargement of the opposing structure. The teeth are distinct and bear a semidenticulate denticular plate. Socket buttresses, lateral to the base of the cardinal process, are fixed along their length to the internal surface of the valve. The socket buttresses are reinforced by a socket plate. The lateral, free edge of the socket buttresses is corrugated to complement the semidenticles of the teeth. Dental lamellae commonly are present. They are histologically confluent with the palintrope, internal surface of the valve and, if present, muscle bounding ridges. The dental lamellae may recede under the palintrope or may be encased in secondary deposits. Prominent dorsal septa are present in older species; they are reduced, modified or absent in younger species. The diductor muscle scars are large and flabellate in most concavo-convex species and small and restricted by a muscle bounding ridge in most plano-convex, biconvex and resupinate species. The pedicle foramen of adults may be open or sealed. According to authors, the lophophore was spirolophous.

*Age.* — Ordovician (lower Chazy, Whiterock) into Mississippian.

*Remarks.* — The origin of the Strophomenacea lies most certainly within the Plectambonitacea but a convincing progenitor has not been discovered. The meso-cardinal ridge between the lobes of the cardinal process of some strophomenaceans is a superficial appendage. The Strophomenacea may not be related to those plectambonitaceans which bear a trifid cardinal process on the basis of the meso-cardinal ridge. Pseudopunctation of certain clitambonitoids can be regarded only as coincidental. There is no evidence of evolutionary relationship between these clitambonitoids and the Strophomenacea.

The *Treatise* incorporates the superfamily Stropheodontacea Caster into the Strophomenacea as the family Stropheodontidae. The number of stropheodontacean genera (38) rivals the number of strophomenacean genera (42). The morphological diversification, geographic distribution and stratigraphic range of the Stropheodontacea is as great as that of the Strophomenacea. The astonishing homeomorphy of genera indicates only that the groups are closely related. In fact, the earliest genera of the Stropheodontacea, *Eostropheodonta, Protomegastrophia,* and *Eostrophonella,* are not clearly differentiated from some strophomenaceans. All strophomenaceans possess a denticular plate in each tooth which is the homologue of the attenuated denticular plate along the free edge of the palintrope of stropheodontaceans. It is the loss of true teeth and the elongation of the denticular plate along the hinge, not just the possession of a denticular plate, which is the true differentium of the Stropheodontacea.

The evidence suggests that a greater degree of difference exists between the stropheodontid group and the families of the Strophomenacea *s.s.* than between any of the families of the Strophomenacea *s.s.*. The rank of the stropheodontid group is clear; it is a superfamily derived from the Strophomenacea. The superfamily Orthotetacea (Davidsoniacea of the *Treatise*) is collateral with the Stropheodontacea in having been derived from the Strophomenacea.

The Stropheodontacea and Strophomenacea do not display heterochronous parallel evolution as would seem to be indicated upon first consideration of the groups. The sequence of evolutionary stages through which some of the features of the Stropheodontacea progress is the inverse of the evolutionary sequence for these features in the Strophomenacea. For example, the stropheodontaceans show enlargement of the pseudodeltidium and reduction of the chilidium with evolutionary advance whereas the strophomenaceans show reduction of the pseudodeltidium and enlargement of the chilidium. The stropheodontacean cardinal process progresses from the conjunct condition to the disjunct condition whereas the strophomenacean cardinal process progresses from disjunct to conjunct. The earliest stropheodontaceans, mentioned above, have closest affinities to moderately advanced strophomenaceans, for example, *Kjaerina* and *Hedstroemina*. Thus, it is not strange that advanced strophomenaceans should have heterochronous homeomorphs in primitive and moderately advanced stropheodontaceans.

*Christiania* cannot be placed in the phylogeny of the Strophomenacea. The genus does possess a bifid cardinal process which is the only diagnostic feature of the Strophomenacea also possessed by *Christiania*. The cardinal process of *Christiania* does not resemble in shape the cardinal process of any true strophomenacean. In fact, the cardinal process of *Christiania* most closely resembles the bilobed, shelflike cardinal process of the thecideoids (*Thecidella*), some of the advanced orthotetids (*Streptorhynchus*) and the thecospirids (*Thecospira*). Other features, for example, the pseudopuncta, socket buttresses and pseudodeltidium require inclusion of *Christiania* into the strophomenid complex but not necessarily into the Strophomenacea. The shape of *Christiania,* the form of the ventral muscle field, the unique dorsal septa and the digitate vascular markings are completely foreign to the Strophomenacea. Spjeldnaes (1957) made a strong case for inclusion of *Christiania* into the Plectambonitacea. On the basis of nonplectambonitacean shape, cardinal process, and dorsal septa of *Christiania,* this genus is regarded as typifying a new superfamily, the Christianiacea. The Christianiacea is probably a derivative of the plectambonitacean complex. The new superfamily mimics the Strophomenacea in possession of a bifid cardinal process but in all other respects is a unique strophomenoid.

Williams (1965, pp. H368-H369) discussed the forms of the lophophores borne by strophomenid brachiopods. He tentatively proposed that certain of the Plectambonitacea were schizolophous or ptycholophous, that *Christiania* was schizolophous and that the rest of the strophomenid brachiopods, including the Strophomenacea, Davidsoniacea, Productidina, and certain plectambonitaceans, were spirolophous. Williams' suppositions seem appropriate considering the lowly evolutionary position generally assigned to the strophomenids among the orders of brachiopods. Moreover, the unquestionable spire of the orthotetacean *Thecospira,* the spiral ramp in the ventral valves of the orthotetacean *Davidsonia verneuili* Bouchard and the plectambonitacean *Leptaenisca jukesi* (Davidson), support the supposed spirolophe of the Strophomenidina. Unfortunately, the form of the lophophore with specific reference to the Strophomenacea and Productidina is not certain.

The internal surface of the dorsal valve of *Leptaenisca concava* Hall bears paired serpentine ridges and the same surface of many productoids and strophomenaceans bear asymmetrical paired ridges or septa, the brachial ridges or dorsal septa. These ridges may be regarded either as "pads" which served for support of the lophophore or as "spacers" which separated the various segments of the lophophore and which may have channeled water into the lophophore apparatus. If hypothetical lophophores are drawn upon the serpentine ridges of *Leptaenisca,* the brachial ridges of a productoid or the dorsal septa of a strophomenacean, a spirolophe is not formed regardless of whether the ridges are considered "pads" or "spacers". Hypothetical lophophores constructed upon the serpentine ridges of *Leptaenisca* are either schizolophous or plectolophous. Hypothetical lophophores constructed upon the brachial ridges and dorsal septa of productoids and strophomenaceans are either ptycholophous or plectolophous. These strophomenids probably possessed the simpler lophophore systems, that is, they probably were schizolophous or ptycholophous.

The marginal diaphragm of the Strophomenacea does not seem to be homologous to the concentric dorsal ridge of the Plectambonitacea. Kozłowski (1929) and Öpik (1930) proposed that the concentric dorsal ridge of plectambonitaceans supported a schizolophe. Sagittal thin sections show that the marginal diaphragm of strophomenaceans could not have been a lophophore support; there was not enough space between the valves at this position. In all probability, the marginal diaphragm was a strainer device, as in the productoids, and may have been a posterior and medial retaining wall for the marginal coelomic canal in the marginal chamber.

### Family **OEPIKINIDAE** Sokolskaya, 1960

*Diagnosis.* — Finely pseudopunctate strophomenaceans with concavo-convex profiles, prolate to subrectangular shape and prominent dorsal septa or standing plates.

*Description.* — The cardinal process lobes are low, generally posteriorly curved shafts or hemicylinders with a cupped myophore on the posterior faces. The teeth are stout and semidenticulate. The socket buttresses generally are straight and possess deeply corrugated lateral margins. The pseudodeltidium and chilidium are variable in size. Older species bear large pseudodeltidia and small chilidia; younger species bear small pseudodeltidia and large chilidia. The chilidium commonly possesses a drape which unites with the meso-cardinal ridge. The posterior platform is strongly developed. A breviseptum is present but may be buried in secondary shell tissue. The diductor muscle scars are flabellate and generally lack muscle bounding ridges. The marginal diaphragm is prominent on the internal surface of the dorsal valve. The pedicle foramen is open in older genera, sealed in younger genera.

*Age.* — Ordovician (lower Chazyan, Whiterock to Richmondian).

*Generic content.* — *Oepikina* Salmon, 1942; *Kirkina* Salmon, 1942; *Dactylogonia* Ulrich and Cooper, 1942; *Hesperinia* Cooper, 1956; *Macrocoelia* Cooper, 1956; *Maakina* Andreeva, 1961.

*Remarks.* — The Oepikinidae is the primitive family of the Strophomenacea from which other families have been derived. The Leptaenidae differs from the Oepikinidae by gradual deletion of the dorsal septa, coarse pseudopuncta, development of various elaborations of geniculation and rugation and restriction of the diductor muscle field. The Rafinesquinidae and Strophomenidae share a common derivation from the Oepikinidae. The Rafinesquinidae retains the concavo-convex shape of the Oepikinidae but deletes the dorsal septa and acquires coarse pseudopuncta. The Strophomenidae are little more than plano-convex to resupinate oepikinids with mechanical modifications, as muscle bounding ridges and receding dental lamellae, required by their profile.

The Oepikinidae of this study and the Oepikinae of the *Treatise* differ in inclusion (here) of *Dactylogonia* and *Hesperinia* and exclusion (here) of *Colaptomena. Dactylogonia* and *Hesperinia* are closely related if not synonymous. Specimens of *Hesperinia,* the oldest strophomenacean, are too poorly preserved to permit complete analysis. *Hesperinia* is not related to the glyptomenid complex as indicated in the *Treatise.* Apparently *Hesperinia* has been compared to *Glyptomena parvula* Cooper [= *Cyphomena* ? *parvula* (Cooper)], a leptaenid, not to *Glyptomena sculpturata* Cooper, type species. *Dactylogonia* and *Hesperinia* are transitional between the Oepikinidae and the Leptaenidae. Their inclusion in one family or the other is largely arbitrary provided they both receive the same allocation. These genera are placed in the Oepikinidae because of the finely pseudopunctate structure of *Dactylogonia* and the prominent dorsal septa or standing plates of both genera.

*Colaptomena* and *Macrocoelia* are closely related genera which are transitional between the Oepikinidae and the Rafinesquinidae. *Macrocoelia* is judged to be an oepikinid because it possesses fine pseudopuncta and small dorsal ridges. *Colaptomena* is placed in the Rafinesquinidae because the genus is coarsely pseudopunctate, bears no stronger dorsal ridges than any rafinesquinid and has a large diductor muscle field. The diductor muscle field of the archaic oepikinids tends to be small and restricted by lateral bounding ridges in the fashion of the leptaenids. Advanced oepikinid genera, *e.g. Oepikina* and *Macrocoelia,* have larger diductor muscle fields which tend to completely surround the adductor muscle scars. Nevertheless, the diductor fields of these advanced oepikinids are smaller and more deeply impressed than the diductor muscle field of the Rafinesquinidae.

*Kirkina,* the second oldest strophomenacean, is known from only one poorly preserved specimen of the internal surface of the dorsal valve and several specimens of external surfaces. *Kirkina,* as *Macrocoelia,* lies along the lineage connecting the Oepikinidae and Rafinesquinidae. *Kirkina* has fine pseudopuncta and reduced dorsal septa and consequently is a phylogenetically advanced oepikinid. *Kirkina* indicates that either the age of the Oil Creek Shale of Millard Co., Utah, is younger than lower Chazyan (Whiterock) or that the base of the strophomenacean phylogeny is older and more complex than can be documented at this time.

### Family **LEPTAENIDAE** Hall and Clarke, 1894

*Diagnosis.* — Coarsely pseudopunctate, coarsely taleolate strophomenaceans with biconvex or concavo-convex, subrectangular, oblate, rarely prolate valves, variously developed geniculation and rugation, modified, reduced or absent dorsal septa, open pedicle foramen and pronounced pseudodeltidium present in older species and small restricted diductor muscle field with adductor muscle scars open to the anterior.

*Description.* — In addition to the diagnostic features, the cardinal process lobes of the leptaenids are low, stout nodes or shafts in older genera to blades with petaloid or cupped, posteriorly facing myophores in younger genera. Older genera lack a meso-cardinal ridge, younger genera possess a meso-cardinal ridge which may be united to the chilidium. The chilidium of older genera is small; the chilidium of younger genera is large, commonly domed and protrusive. A pedicle callist commonly occurs in place of a pseudodeltidium among younger species. The teeth are semidenticulate. The socket buttresses are straight and corrugated along their lateral margins. Dental lamellae are recessive immediately under the teeth but merge with the muscle bounding ridge of the diductor muscle scar. The diductor muscle scar is generally small. The muscle bounding ridge of the diductor muscle scar is weakly to strongly developed and commonly present only along the lateral margins of the muscle scars. If the muscle bounding ridge occurs along the anterior margin of the muscle scars, the muscle bounding ridge is drawn out toward the anterior to produce a lanceolate or petaloid shape. The posterior platform is strongly developed. The adductor muscle scars of the dorsal valve of older genera which bear weak dorsal ridges are obscure. Younger genera which lack dorsal ridges have circular adductor muscle scars in the dorsal valve. The circular adductor muscle scars are formed by the lateral and anterior curvature of the lateral ridges of the posterior platform. The medial ridge of the posterior platform of younger genera bifurcates anterior to the anterior edge of the adductor muscle scars to form a circular depression or low platform. Prominent endospines and dorsal marginal diaphragm generally are present.

*Age.* — Ordovician (lower Champlainian, Ashby) into Mississippian.

*Remarks.* — The Leptaenidae may be divided into three subfamilies, the Leptaeninae with dorsal geniculation and concentric rugae, the Leptaenoideinae with a cemented habit and the Murinellinae with elaborate prosopon, unusual geniculation and reduced or modified dorsal ridges. The Leptaenidae of this classification differs from the Leptaenidae of the *Treatise* by division of the family into subfamilies, incorporation of the Leptaenoideinae which the *Treatise* places in the Strophomenidae, and incorporation of *Murinella* and *Megamyonia.*

### Subfamily **MURINELLINAE**, new

*Diagnosis.* — Primitive leptaenids possessing reduced or modified dorsal septa, elaborate prosopon and unusual geniculation.

*Description.* — The murinellins possess glyptomenoid, ptychoglyptoid, nervose or rarely rafinesquinoid prosopon which is commonly combined with weak concentric to oblique rugae. The profile varies from biconvex to plano-convex with dorsal geniculation or multiple geniculation. If dorsal ridges are present, they appear to be smeared or flattened against the internal surface of the valve. A prominent marginal diaphragm occurs in the dorsal valve.

*Age.* — Ordovician (Champlainian, Ashby into Trentonian).

*Generic content.* — *Murinella* Cooper, 1956; *Cyphomena* Cooper, 1956; *Bellimurina* Cooper, 1956; *Limbimurina* Cooper, 1956; questionably *Oslomena* Spjeldnaes 1957.

*Remarks.* — The Murinellinae is the ancestral group of the Leptaenidae. *Murinella* is related structurally to *Dactylogonia* and *Hesperinia,* thus *Murinella* is one of the least advanced of all strophomenaceans. All specimens of *Murinella* examined by the writer are silicified with the consequence that details of the pseudopuncta are not known. If *Murinella* should prove to be finely taleolate, the genus should be placed in the Oepikinidae. *Murinella* is placed in the Furcitellinae in the *Treatise.* Except for the biconvex to plano-convex profile of *Murinella,* this allocation cannot be supported.

The familial assignment of *Oslomena* cannot be determined satisfactorily. *Oslomena* may be closely related to *Cyphomena* of the Murinellinae or synonymous with *Glyptomena* of the Furcitellinae. Williams' discussion (1962) did not solve the position of *Oslomena* because he does not indicate whether he compared *Oslomena osloensis* Spjeldnaes, type species, to *Glyptomena sculpturata* Cooper, type species, or to *Glyptomena parvula* Cooper [= *Cyphomena* ? *parvula* (Cooper)]. The internal surface of the dorsal valve of *O. papilio* Spjeldnaes resembles that surface of *Bellimurina charlottae* (Winchell and Schuchert), and supports the murinelline assignment of *Oslomena.*

### Subfamily **LEPTAENINAE** Hall and Clarke, 1894

*Diagnosis.* — Leptaenids with subrectangular to subtriangular shape, dorsal or rarely ventral geniculation, concavo-convex or rarely biconvex profile, weak to strong concentric rugae, poorly defined or no true dorsal ridges.

*Description.* — All older leptaenids have subrectangular to subtriangular shapes with pronounced alae; younger species may be oblate or prolate. All older species possess simple dorsal geniculation; younger species may be biconvex or ventrally geniculate, with or without a tongue. Most species bear regularly spaced, concentric rugae on the visceral disk but not on the trail. The fine prosopon of the external surface is rafinesquinoid, nervose or dictyostrophioid. The pseudodeltidium is commonly small to obsolete, rarely large and prominent. The chilidium is protrusive, thin and united with the posterior base of the meso-cardinal ridge. The cardinal process lobes are blades with cupped or petaloid myophores directed toward the posterior. The lobes of the cardinal process of young species (Devonian and Mississippian) may be so conjunct as to form a shelflike structure. The socket buttresses are low, straight, and short. True dorsal ridges are obscure or absent but there may be adventitious ridges or erractic ridges formed by the coalescence of recumbent endospines. The dental lamellae are low, receding and commonly obscured by filling of the umbonal cavities with secondary shell tissue. A pedicle callist is present at the apex of the delthyrial cavity of young species which do not possess an open pedicle foramen. The diductor muscle scars are enclosed, laterally or completely, by muscle bounding ridges. The muscle bounding ridges commonly are drawn-out toward the anterior. The internal surfaces of the valves bear recumbent endospines and pronounced marginal diaphragms. The pedicle foramen is open or sealed.

*Age.* — Ordovician (Champlainian, Porterfield) into Mississippian.

*Generic content.* — *Leptaena* Dalman 1828; *Kiaeromena* Spjeldnaes, 1957; *Leptagonia* McCoy, 1844; *Leptaenella* Frederiks, 1917; *Bekkeromena* Roomusoks, 1963; *Notoleptaena* Gill, 1951; *Rugoleptaena* Havlíček, 1956; *Megamyonia,* Wang, 1949, *Kjerulfina* Bancroft, 1929.

*Remarks.* — The subfamily Leptaeninae contains all of the well-known species associated with the family. The group has a long and complex history in brachiopod taxonomy. In older classifications, the names Leptaenidae and Rafinesquinidae signified identical groups of genera. The genera of these two families, as they are now differentiated, have many similar attributes, for example, the reduced pseudodeltidium, petaloid cardinal process lobes, large taleolae and lack of dorsal septa. These similarities are isophenes in parallel evolving lineages. Because of the parallelism, the familial assignments of several genera are uncertain.

The relationship of *Bekkeromena* to the Leptaeninae is not certain. The shape and curvature of the valves, the posterior platform and the adductor muscle scars of the dorsal valve relate this genus to the Rafinesquinidae. The protrusive chilidium, pedicle callist, attenuated muscle bounding ridges lateral to the diductor muscles and low, obscure dental lamellae are leptaenid features. The leptaenid features are judged to be more strongly developed and of greater significance than the rafinesquinid features.

*Megamyonia* is placed in the Rafinesquinidae in the *Treatise.* The subtriangular to oblate shape, dorsal geniculation, recumbent teeth and round adductor muscle scars in the dorsal valve indicate relationship to the Leptaenidae. The large diductor muscle scars which lack muscle bounding ridges and absence of rugae are rafinesquinid characters.

*Kjerulfina* is a most unusual leptaenid. Externally, *Kjerulfina* is a rugose, ventrally geniculate homeomorph of the rugose, dorsally geniculated rafinesquinid *Kjaerina.* Despite the rugae and geniculation which in this case have no significance, *Kjerulfina* is a leptaenid and not a rafinesquinid because the genus has leptaenoid diductor and adductor muscle scars in the ventral valve, receding dental lamellae, a pedicle callist, circular adductor musce scars in the dorsal valve and short socket buttresses. Internally, *Kjerulfina* closely resembles *Actinomena* of the Furcitellinae but *Kjerulfina* bears coarse pseudopunctae. The kjaerinoid costa of *Kjerulfina* and *Megamyonia* seems to have no taxonomic significance. In spite of all observations, the taxonomic position of *Kjerulfina* is not settled.

### Subfamily **LEPTAENOIDEINAE** Williams, 1953

*Diagnosis.* — Small, subrectangular, concavo-convex leptaenids with dorsal geniculation, which cemented the medial-posterior region of the ventral valve to a foreign object.

*Description.* — The Leptaenoideinae includes small strophomenaceans with leptaenid shape and a cemented habit. The pseudopuncta are coarse and widely spaced. The prosopon is rafinesquinoid to glyptomenoid, with faint rugae, many major varices and distortion caused by the cemented habit. The cardinal process lobes are low, irregular nodes without a distinct myophore. There is no mesocardinal ridge. The socket buttresses are short, straight, thick ridges which are directed anterior-laterally from the lateral margin of the cardinal process nodes. The posterior platform does not bear distinct lateral ridges. The medial ridge of the posterior platform is medially grooved and bears an alveolus at its anterior termination. A breviseptum extends toward the anterior from the alveolus. A serpentine coiled ridge extends laterally from the medial ridge of the posterior platform. The semidenticulate teeth are supported by low, receding to obsolete dental lamellae. The faint dental lamellae merge with muscle bounding ridges along the lateral margins of the diductor muscle scars. A prominent medial ridge bisects the diductor muscle scars and the delthyrial cavity. The pseudodeltidium is small, thick and crudely formed. The interior of the ventral valve bears many beadlike papillae. There is a pedicle foramen in juvenile specimens.

*Age.* — Upper Silurian into Lower Devonian.

*Generic content.* — *Leptaenoidea* Hedström, 1917; *Leptaenisca* Beecher, 1890.

*Remarks.* — The name of this subfamily is poorly chosen because the interior of the dorsal valve of *Leptaenoidea* is unknown. The subfamily Leptaenoideinae is placed in the family Strophomenidae by the *Treatise.* This assignment cannot be supported by any feature or structure. The leptaenoideins are leptaenids by virtue of their shape and profile, coarse pseudopunctae, teeth, obscure dental lamellae and muscle bounding ridges. The interior of the dorsal valve of *Leptaenisca* does not resemble that of any known strophomenacean. When more is known about this curious group, it probably will be necessary to place it in a separate superfamily.

The coiled ridges of the brachial valve may have been callosities for support of a spirolophous lophophore as has been suggested by Muir-Wood (Muir-Wood and Cooper, 1960, p. 20). If this is true, these ridges are the only indication of the shape of the strophomenacean lophophore. The coiled ridges do not seem to be homologues of the dorsal septa of the oepikinids. The microstructure of the coiled ridges is not known.

The stropheodontacean *Liljevalia gotlandica* Hedström has been placed by authors in the Leptaenoideinae. *L. gotlandica* is a true stropheodontacean. The curious perforations of the ventral interarea of this species are caused by accidental rupture of thin shell at the apices of the umbonal cavities and not by perforation of the pseudodeltidium by the cardinal process lobes.

### Family **RAFINESQUINIDAE** Schuchert, 1893

*Diagnosis.* — Coarsely pseudopunctate strophomenaceans with concavo-convex, nongeniculate or dorsally geniculate profile, prolate to subtriangular shape, distinct dental lamellae, adductor muscle scars encircled by large diductor muscle scars in the ventral valve, no dorsal septa and no muscle bounding ridges marginal to the diductor muscle scars.

*Description.* — The rafinesquinids bear coarse, regularly spaced pseudopuncta. The prosopon is rafinesquinoid or glyptomenoid, with or without oblique or concentric rugae and a kjaerinoid costa. The profile is concavo-convex and smoothly curved to indecisively geniculate. The pseudodeltidium is greatly reduced; the chilidium is large, thin, and recumbent upon the posterior bases of the cardinal process lobes. The cardinal process lobes are bladelike in older species and juveniles to massive and petaloid in young species. There is no meso-cardinal ridge in juveniles and older species. The socket buttresses are long, straight and deeply corrugated along the free edge. The posterior platform is anchor-shaped to arrowhead-shaped. The medial ridge of the posterior platform does not extend far anterior of the adductor muscle scars and does not bifurcate. A breviseptum is rarely present. The adductor muscle scars of the dorsal valve are not circular. The semidenticulate teeth are supported upon distinct, thin, nonreceding dental lamellae. The dental lamellae rarely are prolonged to the anterior to form weak muscle bounding ridges on the posterior-lateral margin of the diductor muscle scars. The diductor muscle scars are large and flabellate. The adductor muscle scars of the ventral valve are situated near the center of the diductor muscle scar area. The pedicle foramen is generally sealed, rarely minute and supra-apical. Endospines and a marginal diaphragm are weakly to strongly developed.

*Age.* — Ordovician (upper Chazy, Ashby) into Lower Silurian.

*Generic content.* — *Rafinesquina* Hall and Clarke, 1892; *Colaptomena* Cooper, 1956; *Pionomena* Cooper, 1956; *Kjaerina* Bancroft, 1929; *Hedstroemina* Bancroft, 1929.

*Remarks.* — The Rafinesquinidae is a distinctive family which arose from a *Macrocoelia*-like ancestor by deletion of the dorsal septa and enlargement of the pseudopuncta. *Rhipidomena* of the Furcitellinae is so closely related to *Macrocoelia* that *Rhipidomena* could be considered a rafinesquinid if it were not finely pseudopunctate and gently resupinate. As noted, *Colaptomena* possesses coarse pseudopuncta and lacks dorsal septa. In other respects, *Colaptomena* closely resembles *Macrocoelia.* This would indicate that the coarsely pseudopunctate condition arose abruptly and without related structural change.

The type species of *Kjaerina* and *Hedstroemina* are distinct. Other species of these genera seem to be intergradational. Whether these genera are distinct but partly homeomorphic or truly intergradational has not been established.

The generic assignment of the late Ordovician species of *Rafinesquina* was questioned by Salmon (1942). The late Ordovician species have no relationship to *Longvillia,* contrary to her suggestion. The number of species of *Rafinesquina* is so great that there are no prominent discontinuities in the morphogenesis of the genus. If the record of this genus were incomplete, the early Trentonian species and the Cincinnatian species would probably be placed in separate genera.

*Pionomena* is known from several casts of the external surface of the valves and one poorly preserved internal surface of the posterior region of the ventral valve. *Pionomena* is tentatively placed in the Rafinesquinidae on the basis of external appearance, prominent teeth, well-developed dental lamellae and coarse pseudopuncta.

### Family **STROPHOMENIDAE** King, 1846

*Diagnosis.* — Finely pseudopunctate, resupinate, biconvex or rarely plano-convex or concavo-convex strophomenaceans with recurved socket buttresses, commonly with receding dental lamellae, restricted diductor muscle scars, true but reduced dorsal ridges or adventitious ridges and a breviseptum from the bifurcate anterior end of the medial ridge of the posterior platform.

*Description.* — The Strophomenidae includes species with every possible strophomenacean shape. The profile commonly is resupinate or biconvex but may be biplanate, plano-convex or concavo-convex in atypical species. The valves have either smoothly curved profiles or ventral geniculation. The anterior margin may be rectimarginate, sulcate or uniplicate. The prosopon generally is strophomenoid or glyptomenoid but every other variety of prosopon known in the Strophomenacea is found. The pseudodeltidium and chilidium are present in all species. The size of the pseudodeltidium varies from large to small; the chilidium is small. The cardinal process lobes are erect cylinders or nodes. The cardinal process myophores of advanced species are cupped or petaloid. Few species have a mesocardinal ridge which, if present, is hidden under the chilidium. The socket buttresses are recurved in the shape of a hunting bow. The posterior-medial ends of the socket buttresses are widely divergent. The lateral ends of the socket buttresses generally merge into the palintrope lateral to the socket. The floor of the socket may be elevated above the nearby region of the internal surface of the valve. The free edges of the socket buttresses are corrugated. The posterior platform is small. The lateral ridges of the posterior platform are short and not sharply curved toward the anterior. The medial ridge of the posterior platform generally is bifurcate. The breviseptum arises in the split end of the medial ridge. The adductor muscle scars of the dorsal valve are indistinct. The internal surface of the dorsal valve may or may not possess true dorsal ridges or adventitious ridges. The teeth are stout. The blunt, semidenticulate anterior end of the denticular plate projects toward the anterior from the free edge of the palintrope. An accessory socket for reception of the lateral socket buttress (= accessory tooth) may occur in the free edge of the palintrope lateral to the denticular plate. The dental lamellae commonly recede under the teeth. The dental lamellae merge into muscle bounding ridges. The muscle bounding ridges vary from short ridges along the lateral-posterior margin of the small diductor muscle scars to ridges which almost surround the diductor muscle scars. The adductor muscle scars are situated near the anterior margin of the diductor muscle field. The adductor muscle scars are not enclosed to the anterior by the diductor muscle scars. Prominent adjustor muscle scars may interrupt the posterior-lateral segments of the muscle bounding ridges. The interior surfaces of the valves may be smooth or may bear papillae or endospines. The marginal diaphragm is weakly to strongly developed. The pedicle foramen is open or sealed.

*Age.* — Ordovician (lower Champlainian, Ashby) to Upper Silurian.

*Remarks.* — The family Strophomenidae is the largest, most complex and most diverse family of the Strophomenacea. There are no absolute differentia for the Strophomenidae but combinations of features permit their recognition. The Strophomenidae arises from a *Macrocoelia*-like oepikinid. The earliest strophomenid, *Rhipidomena,* is a gently resupinate *Macrocoelia.* The Orthotetacea surely arise from the subfamily Furcitellinae.

Other descriptions of strophomenids specify that the muscle bounding ridges arise from the medial surfaces of the dental lamellae and, by inference, are not anterior continuations of the dental lamellae. This interpretation is not correct. The muscle bounding ridges and the dental lamellae are histologically continuous structures. The adjustor muscle scars are impressed into the site where the dental lamellae become ridges. The effect is shown in Text-figure 5, number 4.

### Subfamily **FURCITELLINAE** Williams, 1965

*Diagnosis.* — Biconvex, biplanate resupinate or rarely concavo-convex strophomenids with incomplete muscle bounding ridges, slightly reduced or modified dorsal septa, large pseudodeltidium and an open or sealed pedicle foramen.

*Description.* — The shape, profile, nature of the anterior commissure, and prosopon may be any of the various forms listed for the family. The profile is rarely concavo-convex, geniculate or strongly resupinate. The chilidium is small; the pseudodeltidium generally is large. The cardinal process lobes are nodes in older species. In younger species, the cardinal process lobes are posteriorly bent, low cylinders with cupped myophores in the posterior face. The socket buttresses and posterior platform are those described for the family. True dorsal ridges or standing plates occur in all but the most advanced species. The teeth are more delicate and more pointed than the teeth of the Strophomeninae. The dental lamellae may or may not recede. The diductor muscle field is small and restricted by lateral muscle bounding ridges. The diductor muscle field is not elevated above nearby regions of the internal surface of the valve. The pedicle foramen is open in all but the most advanced species. The internal surfaces of the valves may be smooth or may bear papillae or endospines. The marginal diaphragm is weakly developed.

*Age.* — Ordovician (lower Champlainian, Ashby, to upper Cincinnatian, Richmondian).

*Remarks.* — The Furcitellinae includes the primitive strophomenids as indicated by the presence of true dorsal septa, an open foramen, large pseudodeltidium and great variability of shape, profile and anterior commissure.

### Tribe **GLYPTOMENINI** Williams, 1965

*Diagnosis.* — Weakly plano-convex, biplanate, resupinate or concavo-convex furcitellines with prolate shape, a rectimarginate anterior commissure, weak to absent posterior platform, strong to absent true dorsal septa, incomplete muscle bounding ridges and cylindrical or minute, beadlike cardinal process lobes.

*Age.* — Ordovician (lower Champlainian, Ashby, into Cincinnatian, Maysvillian).

*Generic content.* — *Rhipidomena* Cooper, 1956; *Glyptomena* Cooper, 1956; *Platymena* Cooper, 1956; *Actinomena* Öpik, 1930; *Mjoesina* Spjeldnaes, 1957.

*Remarks.* — The principal distinguishing features of the Glyptomenini are the flat profile and the prolate shape.

The Glyptomenini are the least advanced tribe of the Furcitellinae. There is a major gap in the phyletic record between *Rhipidomena,* the most primitive genus of the tribe, and the succeeding genera, *Glyptomena* and *Platymena. Rhipidomena* is not typical of the tribe by possession of strong, true dorsal septa, cylindrical cardinal process lobes, a large posterior platform, no muscle bounding ridges, and stout teeth. *Rhipidomena* could be considered to typify a monogeneric tribe. *Rhipidomena* is weakly resupinate to biplanate and prolate. Consequently, *Rhipidomena* fits into the Glyptomenini if a hiatus is accepted.

The Glyptomenini are ancestral to the Furcitellini and to the Strophomeninae.

### Tribe **FURCITELLINI** Williams, 1965

*Diagnosis.* — Biconvex, oblate or subtriangular, rectimarginate or uniplicate, coarsely costate furcitellines with strongly to weakly developed true dorsal ridges, incomplete muscle bounding ridges and cardinal process lobes bent toward the posterior.

*Age.* — Ordovician (lower Trenton into upper Cincinnatian, Richmondian).

*Generic content.* — *Furcitella* Cooper, 1965; *Holtedahlina* Foerste, 1924.

*Remarks.* — The most characteristic features of the Furcitellini are the biconvex profile and oblate shape.

*Furcitella* and *Holtedahlina* are similar in all features except for the stronger dorsal ridges of *Furcitella* and the fold of *Holtedahlina.* When middle Trenton species are found, the two genera probably will not be differentiable.

The Teratelasmini probably arises from pre-*Furcitella* species of the Furcitellini.

### Tribe **TERATELASMINI,** new

*Diagnosis.* — Small, oblate, weakly biconvex or concavo-convex furcitellines with prominent anterior dorsal septa, with or without a medial dorsal septum, with widely divergent socket buttresses, uniformly capillate or smooth external surfaces, without muscle bounding ridges, with beadlike or no cardinal process lobes.

*Age.* — Ordovician (middle Champlainian, Porterfield, and upper Cincinnatian, lower Ashgill).

*Generic content.* — *Teratelasma* Cooper, 1956; *Foliomena* Havlíček, 1952.

*Remarks.* — These two strange, minute furcitellin genera differ by the presence of a high medial dorsal septum in *Teratelasma* and the smooth external surfaces of *Foliomena.* The prominent anterior dorsal septa of *Teratelasma* seem to be formed by the fusion of both the anterior and the posterior dorsal septa. There do not seem to be cardinal process lobes on *Foliomena*. This may be an accident of preservation. The differences between *Teratelasma* and *Foliomena* may be explained by the long interval, middle Champlainian to middle Cincinnatian, which separates them. The curious, simplified morphology of these two genera in itself may be indicative of their relationship. Their rarity, lack of species diversification and temporal and geographic separation prevent a complete assessment of this tribe. The genera are not acceptable into any subfamily of the Strophomenacea other than the Furcitellinae and here they show greatest resemblance to the Furcitellini proper.

### Subfamily **STROPHOMENINAE** King, 1846

*Diagnosis.* — Resupinate strophomenids with muscle bounding ridges extended around the anterior margin of the diductor muscle field, true dorsal septa weakly developed to absent, adventitious septa strongly developed to absent.

*Description.* — The Strophomeninae includes strophomenids which generally are strongly resupinate, with or without ventral geniculation. The shape of the valves is prolate, subtriangular, subrectangular or rarely oblate. The prosopon commonly is strophomenoid but may be rafinesquinoid or glyptomenoid. Unusual species have nervose, cymostrophoid or ptychoglyptoid prosopon. Weak concentric or oblique rugae may be combined with any of the common patterns of prosopon. The pseudodeltidium is large, rarely small; the chilidium is small. The cardinal process lobes are slender to stout cylinders which bear a posteriorly directed petaloid or cupped myophore. A meso-cardinal ridge is rarely present. The socket buttresses are recurved toward the interarea on the lateral-posterior side of the socket. Both the socket buttress and the lateral socket buttress are generally corrugated. The posterior platform is small but highly elevated. The medial ridge of the posterior platform generally is bifurcate. A breviseptum may arise in the split end of the medial ridge. True but reduced dorsal ridges transect the adductor muscle field of some species. Thick adventitious or intervascular ridges may occur in the region anterior and anterior-lateral to the adductor muscle scars. Those species with prominent adventitious ridges commonly have breviseptum-like ridges or narrow grooves in the positions of the true anterior dorsal septa and posterior dorsal septa. Some species lack all traces of dorsal septa or adventitious septa. The teeth are stout and semidenticulate on the dorsal surface. A transverse muscle bounding ridge may occur along the anterior margin of the adductor muscle field of the dorsal valve. The dental lamellae commonly recede. The muscle bounding ridges of the ventral valve almost encircle the anterior ends of the small diductor muscle scars. The adductor muscle scars of the ventral valve generally are not enclosed toward the anterior by the muscle bounding ridges. There may be a small spondylium triplex and hemisyrinx in the apex of the delthyrial cavity. The pedicle foramen is sealed but commonly apparent because of differential erosion. The internal surfaces of the valves may be smooth or may bear papillae or endospines. The marginal diaphragm commonly is well developed in the ventral valve.

*Age.* — Ordovician (middle Champlainian, Porterfield) into Upper Silurian.

*Generic content.* — *Strophomena* Rafinesque, *in* De Blainville, 1825; *Tetraphalerella* Wang, 1949; *Longvillia* Bancroft, 1933; *Gunnarella* Spjeldnaes, 1957; *Pentlandina* Bancroft (edited by Lamont) 1949; *Trigrammaria* Wilson, 1945; *Microtrypa* Wilson, 1945; *Luhaia* Roomusoks, 1956.

*Remarks.* — The nomenclatural validity of *Strophomena* is not established. The type species of *Strophomena* is *S. rugosa* Rafinesque, in De Blainville, 1825. Illustrations of *S. rugosa* are unrecognizable; the type specimens apparently are lost. A strict interpretation of the International Code of Zoological Nomenclature would require that *Strophomena* be declared unrecognizable and invalid. Hall and Clarke (1892) and Nickles (1903) reviewed the status of *Strophomena* and the history of the name. Nickles suggested that *Leptaena planumbona* Hall, 1847 [= *S. planumbona* (Hall)] was probably not conspecific with *S. rugosa* Rafinesque as Hall and Clarke (1892) claimed it to be. Nickles concluded, in substance, that this is not significant inasmuch as authors "King, Davidson, Hall and Clarke, Winchell and Schuchert", understood the type of *Strophomena* to be *S. planumbona* (Hall). Authors subsequent to Nickles, *e.g.* Cooper and Williams, also based *Strophomena* upon *S. planumbona* (Hall). The status of *Strophomena* has not been ruled upon by the International Commission on Zoological Nomenclature. The type should be fixed as *Strophomena planumbona* (Hall) by appeal to the commission so that no uncertainty continues.

Unfortunately, the *Treatise* compounds the *Strophomena*-problem. The internal surface of a dorsal valve shown in figure 246, 3c (p. H385) which is identified as *S. planumbona* (Hall) is *S. vetusta* (James).

True dorsal ridges do occur in the Strophomeninae. These are not the thick, adventitious ridges which may be so apparent on the internal surface of the dorsal valve. The true dorsal ridges are slender ridges or faint grooves located between the adventitious ridges. Both the adventitious ridges and the true dorsal ridges may arise in the adductor muscle field. Generally only the medial dorsal ridge, *i.e.* breviseptum, and the anterior lateral dorsal ridges are present. The true dorsal septa are most apparent on slightly eroded or naturally etched calcite specimens because the inner initial tissue which forms the true dorsal ridges is slightly darker in color than the secondary tissue which forms the adventitious ridges.

The nomenclatural validity of *Longvillia* Bancroft and *Pentlandina* Bancroft has been questioned. The obscure publications in which these genera were described, by the fact of their obscurity, have attracted the attention of brachiopod specialists. Consequently, these names must be judged to be acceptably published. *Longvillia* Bancroft is not a synonym of *Strophomena,* as shown in the *Treatise,* if the type species of *Strophomena* is *S. planumbona* (Hall). *Longvillia grandis* (J. de C. Sowerby) type species, has a flattened resupinate profile, delicate teeth, a weakly developed muscle bounding ridge and no dorsal septa.

The differentiation of *Microtrypa* from *Strophomena* is uncertain. The type specimens of *M. altilis* Wilson, type species, are too poorly preserved to permit an adequate diagnosis of this genus.

## OTHER GENERA

The genera of the following list have been at one time assigned to the Strophomenacea. The reason for rejection of each name is indicated.

*Bekkerella* Reed, 1936. — Inadequately known and probably a stropheodontacean.
*Brynella* Bancroft, 1933. — *nomen nudum*
*Christiania* Hall and Clarke, 1892. — Placed in a new superfamily, the Christianiacea.
*Coolinia* Bancroft, *in* Lamont, 1949. — Probably an orthotetacean.
*Drummuckina* Bancroft, *in* Lamont, 1949. — Probably a stropheodontacean.
*Goniotrema* Ulrich and Cooper, 1936. — A plectambonitacean.
*Lamanskya* Moberg and Segerberg, 1906. — Unrecognizable.
*Leptaenella* Sarycheva and Sokolskaya, 1952. — A synonym of *Leptagonia* McCoy, 1844; a homonym of *Leptaenella* Frederiks, 1917.
*Leptaenulopsis* Haupt, 1878. — A synonym of *Leptaena.*
*Oepikinella* Wilson, 1945. — Probably a synonym of *Strophomena.*
*Playfairia* Reed, 1917. — An unrecognizable subgenus of *Rafinesquina.*
*Pseudoleptaena* Miloradovich, 1947. — A synonym of *Leptagonia.*
*Saughina* Bancroft, *in* Lamont, 1949. — Probably an orthotetacean.

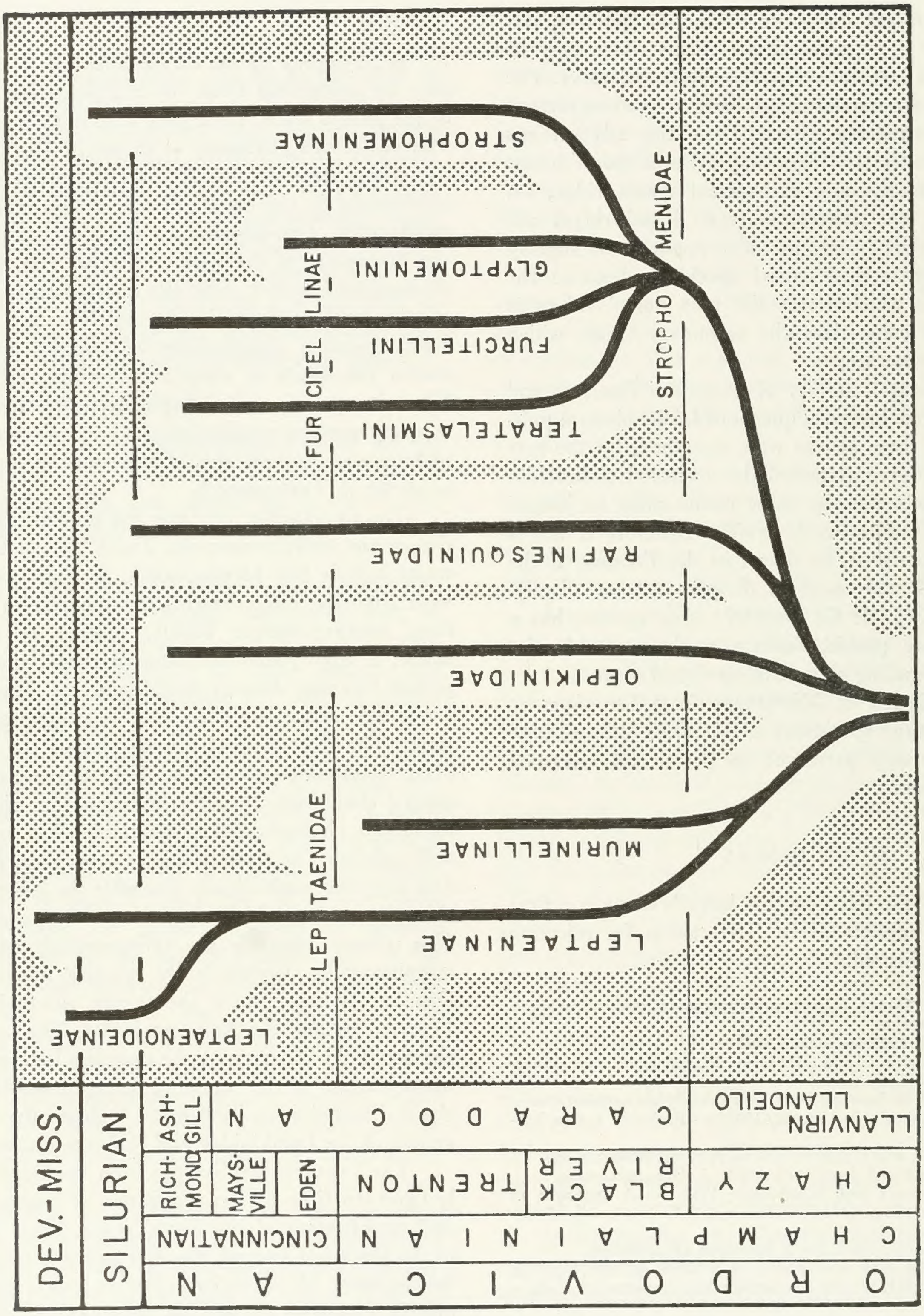
## PHYLOGENY

A phylogeny of the Strophomenacea of the Ordovician may be postulated from the morphological characteristics of the groups which have been described in the last section. The postulated phylogeny is shown in Text-figure 7.

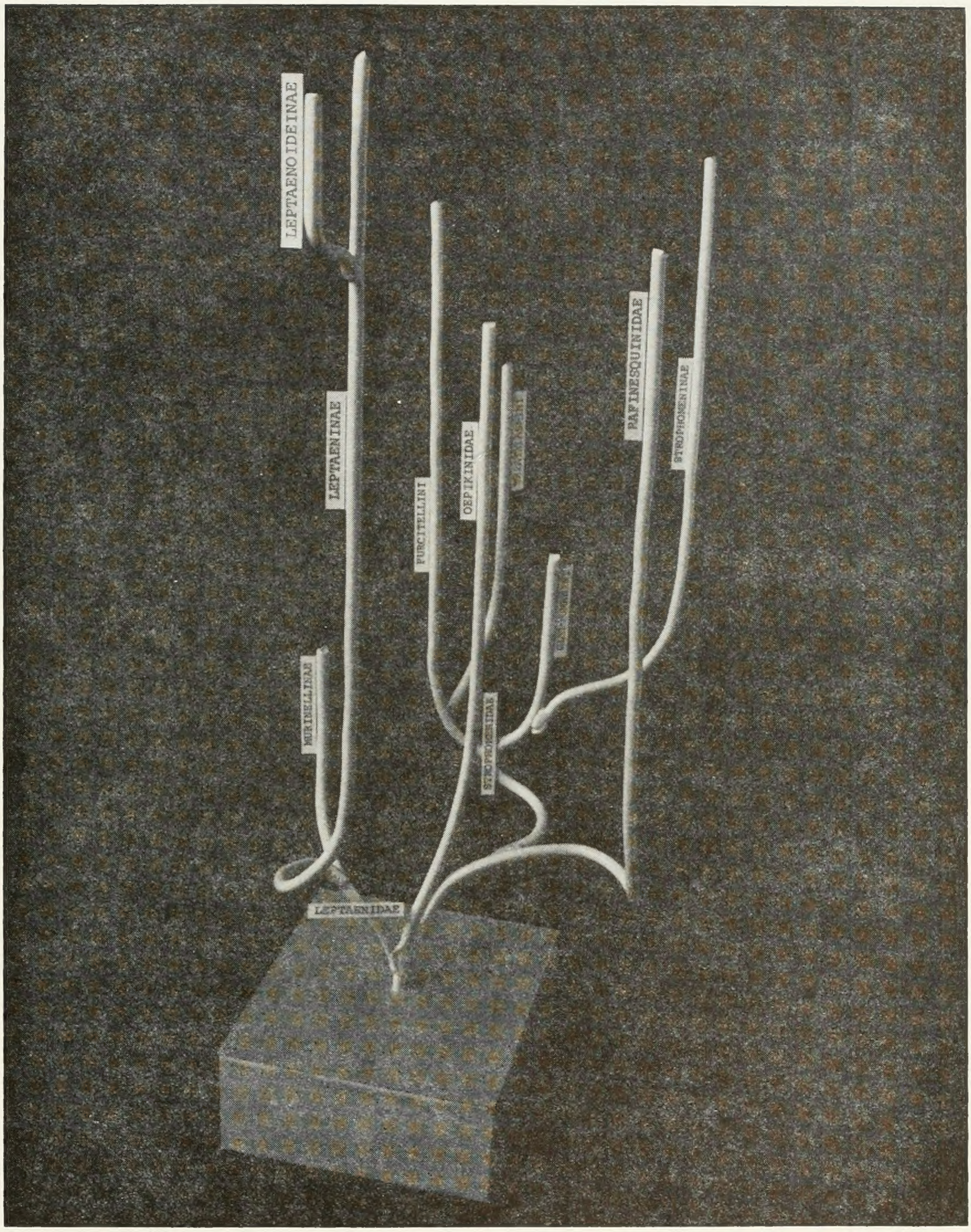
Many dendrograms of the Strophomenacea have been constructed in the course of this study. None are entirely satisfactory. Two-dimensional dendrograms can show only the divergence of the various groups. The two-dimensional dendrograms cannot show the relative degree of divergence of the groups involved nor can they show convergence. Every possible juxtaposition of families and subfamilies, within the limits of their relationships, has been drawn. There is separation of closely related or convergent families in every possible combination. The phylogeny of the Strophomenacea properly should be viewed in three dimensions, as shown in Text-figure 8.

The Oepikinidae contains the fundamental characteristics of the Strophomenacea. These basic strophomenacean traits include fine pseudopuncta, the bifid cardinal process with shaftlike lobes bearing myophores on the posterior face, concavo-convex profile, prolate to subrectangular shape, a large pseudodeltidium with an open, supraapical pedicle foramen, distinct dental lamellae, unrestricted diductor muscle scars, straight socket buttresses and true dorsal septa. The diagnostic characteristics of the other families occur by modification or loss of one or more of these fundamental characters. In a three-dimensional view of strophomenacean phylogeny, the Oepikinidae has an axial or central position. The most primitive oepikinids, *Hesperinia* and *Dactylogonia,* most closely resemble the leptaenids, whereas the advanced oepikinids, *Kirkina, Macrocoelia,* and *Oepikina,* closely resemble the rafinesquinids and the earliest strophomenids. Consequently, graphic illustration of the Oepikinidae must show the family situated between the Leptaenidae and the Rafinesquinidae. The basal portion of the oepikinid lineage must be near the Leptaenidae and the upper portion of the oepikinid lineage must be bent toward the Rafinesquinidae. Text-figure 9 shows the relationship of genera of the Oepikinidae and Rafinesquinidae.

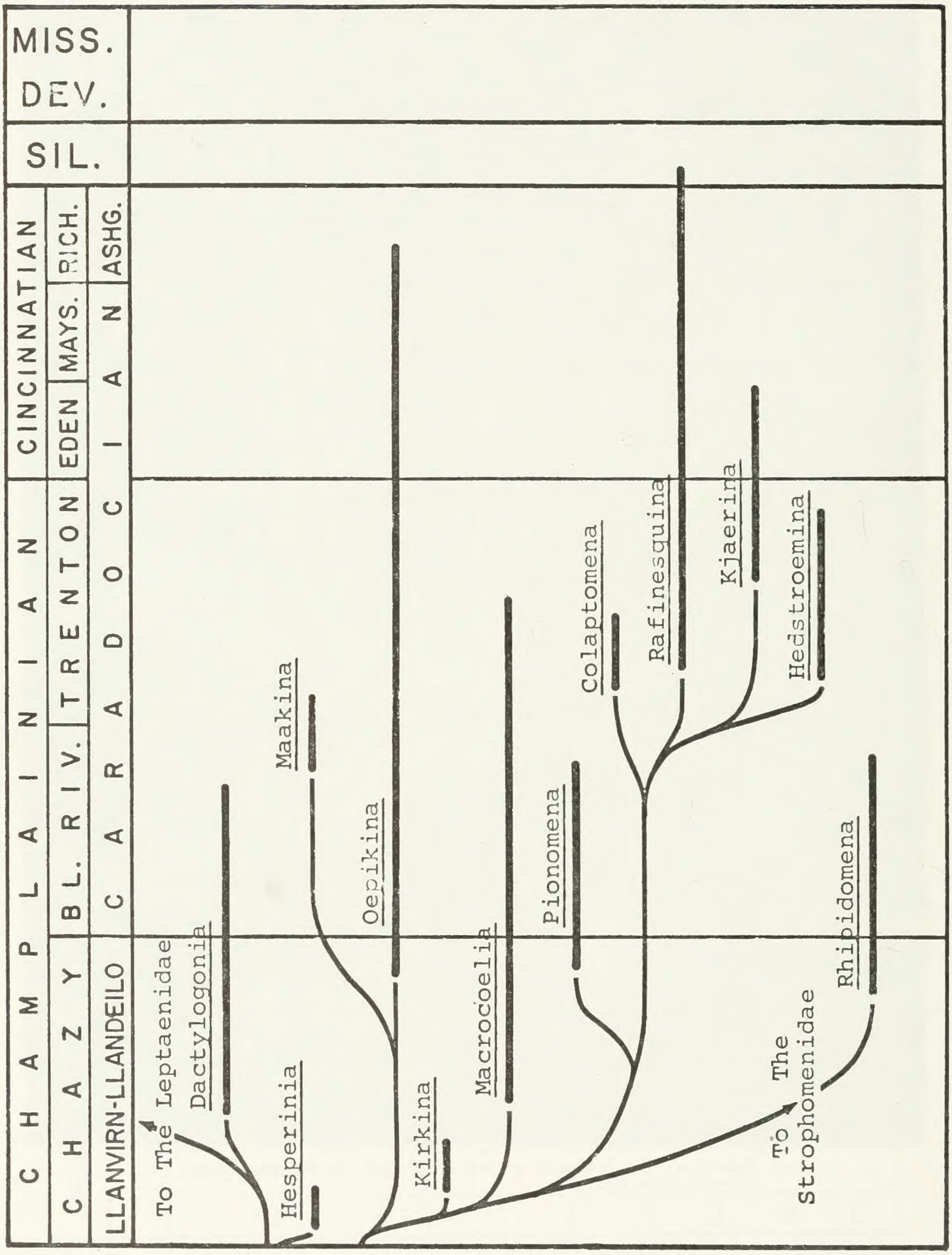
The Leptaenidae diverges from the Oepikinidae in early Chazyan time by the acquisition of coarse pseudopuncta and modification of the dorsal septa. Later in the history of the leptaenid lineage, the divergence is reinforced by the development of strong geniculation, rugae and incomplete muscle bounding ridges, the reduction of dental lamellae and the pseudodeltidium, and further modification or loss



*Text-figure 7.*—The postulated phylogeny of the families of the Strophomenacea.



*Text-figure 8.*— Phylogeny of the families of the Strophomenacea shown in three dimensions.



*Text-figure 9.*—The relationship and stratigraphic distribution of genera of the Oepikinidae and Rafinesquinidae.

of the dorsal septa. The relationship and stratigraphic distribution of genera in the Leptaenidae is shown in Text-figure 10.

The Leptaenidae divides into two subfamilies in Chazyan time. The Murinellinae is distinguished by elaborate geniculation and prosopon and by retention of a foramen, large pseudodeltidium and modified dorsal septa through much of its history. The Murinellinae is a more primitive lineage than the Leptaeninae by reason of these characters and consequently occupies a position between the Oepikinidae and the Leptaeninae. Moreover, the prosopon, posterior platform, socket buttresses and dorsal septa of the Murinellinae resemble those features in the Furcitellinae. A three-dimensional model shows the Murinellinae closer to the Oepikinidae than the Leptaeninae and bent into convergence with the Furcitellinae.

The Leptaeninae diverges further from the Oepikinidae than does the Murinellinae by complete loss of the dorsal septa and reduction of the pseudodeltidium. The Leptaeninae shows some convergence toward the Rafinesquinidae by development of bladed cardinal process lobes which become petaloid, loss of the dorsal septa, reduction of the pseudodeltidium, and in some genera, the shape of the posterior platform, the loss of rugae, geniculation, subrectangular shape and muscle bounding ridges.

The Leptaenoideinae diverges from the Leptaeninae in late Ordovician or early Silurian time. The cemented habit of these minute leptaenids does not occur elsewhere in the Strophomenacea. The Leptaenoideinae, thus, must be imagined to diverge centripetally from the strophomenacean complex.

The Rafinesquinidae diverges from an advanced oepikinid by development of coarse pseudopuncta, loss of the dorsal septa and increase in the size of the diductor muscle field. Also, the petaloid myophores of the most advanced rafinesquinids face in the posterior-dorsal direction unlike the myophores of all oepikinids. In all other characters, the Rafinesquinidae resembles advanced genera of the Oepikinidae which have prolate shape, a sealed pedicle foramen and a reduced pseudodeltidium. As noted, the Rafinesquinidae and the Leptaenidae show some convergent characteristics. A three-dimensional illustration of the Strophomenacea would show these families bent toward each other.

The Strophomenidae arises from the same advanced oepikinid stock as does the Rafinesquinidae. The stratigraphic distribution and relationship of genera of the Strophomenidae is shown in Text-figure 11. The earliest strophomenid, *Rhipidomena,* is so nearly intermediate that only the gentle resupination and obsolete dental lamellae require that the genus be rejected from the Oepikinidae. Moreover, the morphology of *Rhipidomena* places this genus at the bifurcation of the Furcitellinae and the Strophomeninae. *Rhipidomena* is assigned to the Furcitellinae, tribe Glyptomenini, only because the Furcitellinae collectively displays more primitive features than does the Strophomeninae.

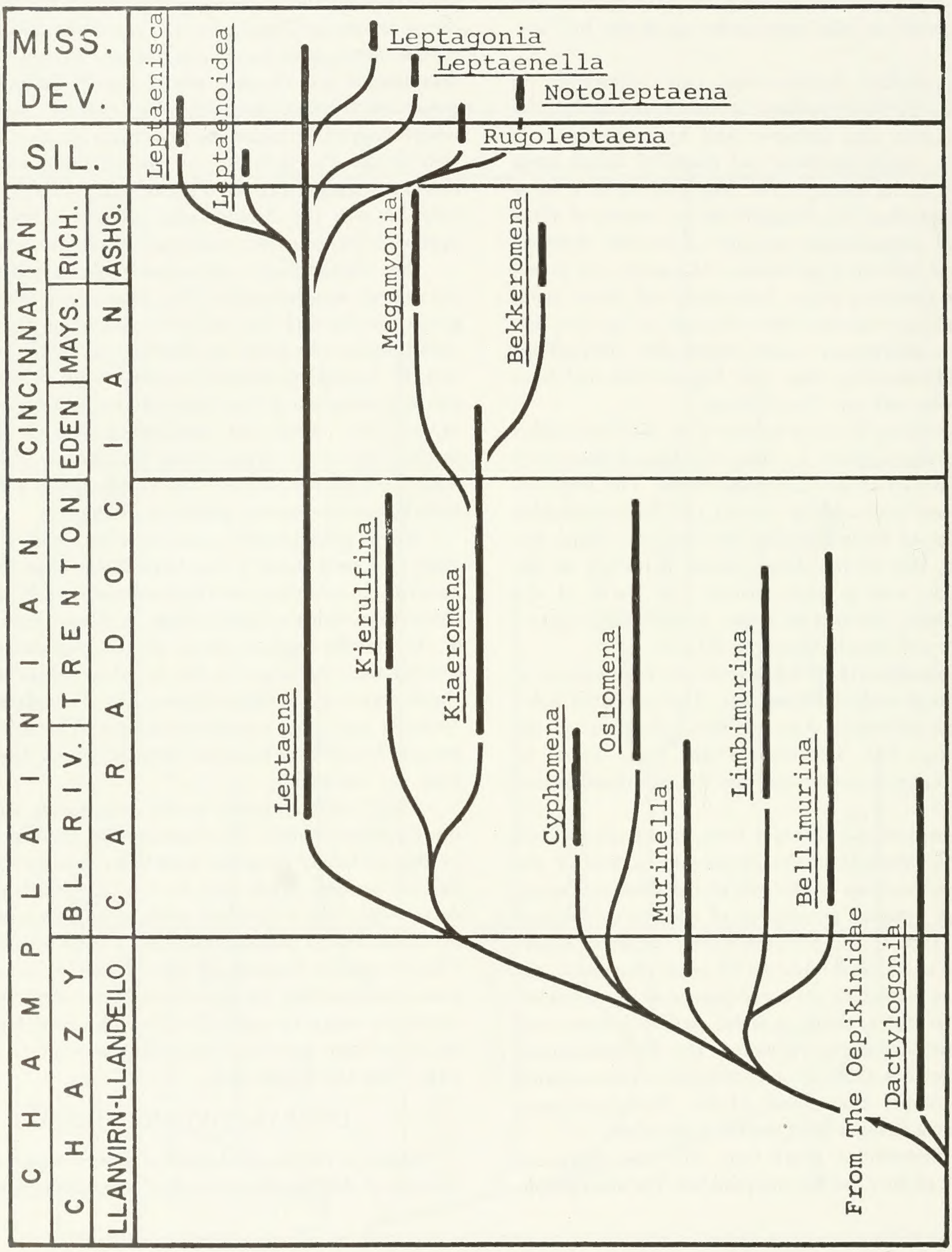
The Furcitellinae encompasses the primitive but experimental strophomenids. The primitive attributes of the group are internal and include features as the prominent dorsal septa, the node or shaftlike cardinal process lobes and the incomplete muscle bounding ridges. The shape, profile, and prosopon of the Furcitellinae are experimental features. They include the flattened profile of the Glyptomenini, the oblate shape of the Furcitellini and Teratelasmini, the biconvex profile of the Furcitellini and *Teratelasma* and the concavo-convex profile of *Foliomena.*

In a phylogenetic reconstruction, the Furcitellinae must be shown closer to the Oepikinidae than the Strophomeninae. In addition, the Glyptomenini and Furcitellini are convergent with the Murinellinae. A three-dimensional view of the strophomenacea shows the Glyptomenini and Furcitellini near the origin of the Strophomenidae and bent in the direction of the Murinellinae. The Teratelasmini do not resemble any other strophomenaceans. This tribe must be imagined to diverge from the Furcitellini in a direction away from the oepikinids.

The Strophomeninae is the progressive subfamily of the Strophomenidae. The fundamental structures retained by this subfamily from the oepikinid origin are fine pseudopuncta, prolate shape and, in less advanced species, the dorsal septa, the cylindrical cardinal process lobes with the myophore on the posterior face and a large pseudodeltidium. The progressive features of the subfamily include the extreme resupination, strong muscle bounding ridges and adventitious septa of many species. The Strophomeninae is divergent from the base of the Glyptomenini in a direction away from the Oepikinidae.

## COMPARATIVE MORPHOLOGY

Many of the morphological and microstructural characteristics of the Strophomenacea change throughout the his-



*Text-figure 10.*—The relationship and stratigraphic distribution of genera of the Leptaenidae.

tory of the superfamily. Morphological variation in the Strophomenacea is summarized in Table 1. Some of the changes seem to be related to changes in the profile of the valves; other changes seem to be independent of the profile. The features which seemingly undergo change without relationship to profile include the size and shape of the valves, pseudopuncta, teeth, diductor muscle scars, prosopon, the cardinal process lobes, the pseudodeltidium, the chilidium, the pedicle foramen, the dorsal septa and the meso-cardinal ridge. Characters which may change collateral to changes of profile include the dental lamellae, the muscle bounding ridges and the socket buttresses. It is convenient to discuss the modifications of these characters in respect to variations of the profile of the valves. The selection of profile as the standard of reference is arbitrary. The characters, including profile, change collaterally. No character has precedence over another; changes of profile are not necessarily a cause which produce an effect in the other characters.

The structures which change without relationship to profile of the valves may be divided into three categories. The shape and profile of the valves, nature of the pseudopuncta, teeth, and diductor muscle scars, in general, are taxonomic differentiae at the familial level. These features do not change through a sequence of evolutionary stages within the superfamily, nor do the variations of these features, in general, occur at random within the superfamily. Changes which occur in the pseudodeltidium, interarea of the ventral valve, chilidium, foramen and dorsal septa are the result of evolutionary parallelism in the various lineages. The cardinal process shows poorly defined taxonomic differentiation and evolutionary progression. Size, nature of the prosopon, adductor muscle scars, and occurrence of a meso-cardinal ridge do not seem to have much taxonomic or evolutionary significance above the generic level. Vascular markings are too obscure to be evaluated.

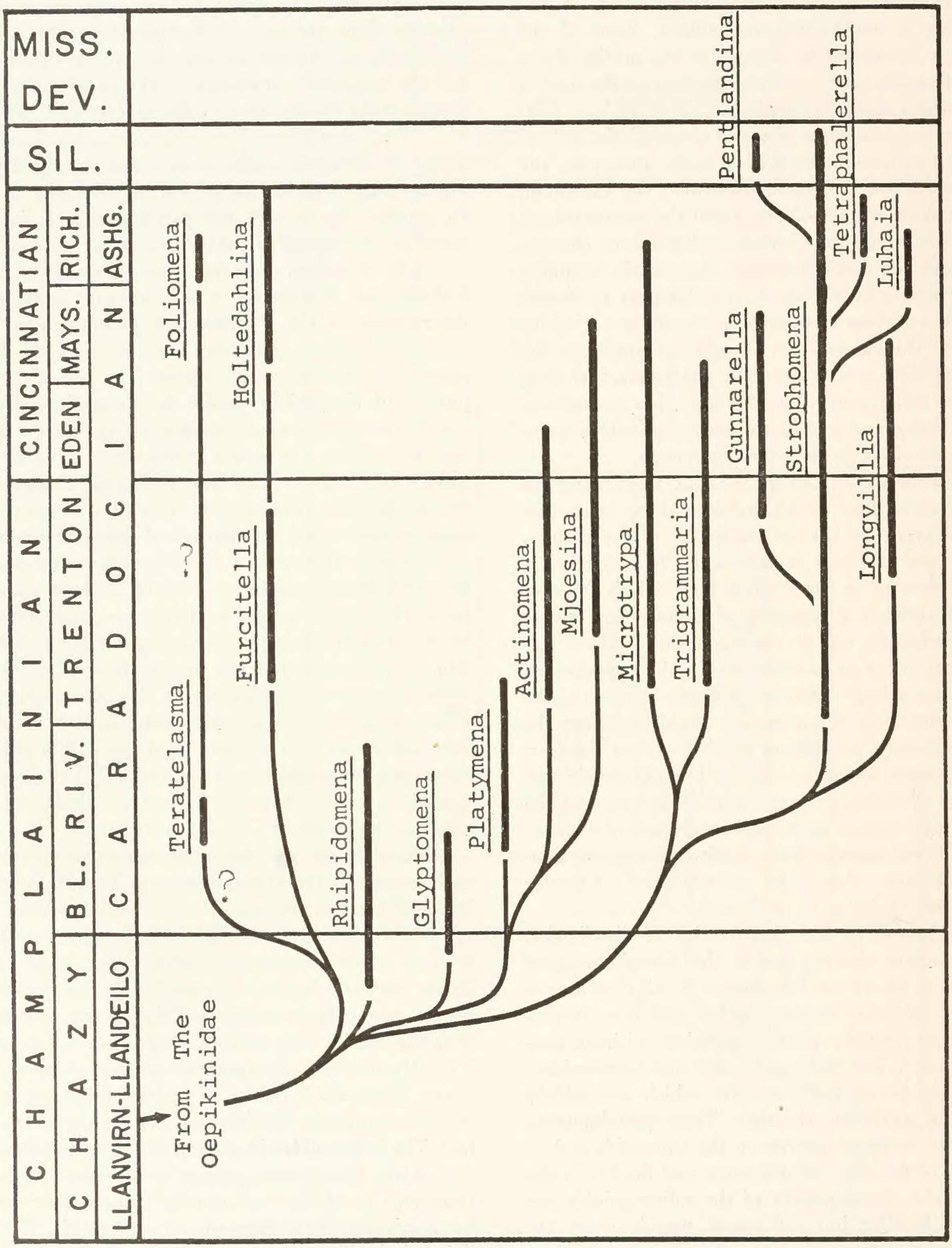
*Pseudopuncta.* — The size and density of distribution of the pseudopuncta sharply divide the Strophomenacea into two groups as shown on Text-figure 12. All members of the Oepikinidae and the Strophomenidae bear fine pseudopuncta which are densely packed together without geometric arrangement. The Rafinesquinidae and Leptaenidae, in contrast, bear coarse pseudopuncta which are widely and geometrically spaced in the shell. These pseudopuncta occur along the intercostal grooves in the leptaenids and at the intersection of the intercostal grooves and the fila in the rafinesquinids. The pseudopuncta of the rafinesquinids are bimodal in size. Smaller, but still coarse, pseudopuncta are scattered at random among the geometrically placed larger pseudopuncta. The rafinesquinids and leptaenids bear taleolae along the axes of the pseudopuncta. Most of the oepikinids and strophomenids seem to be taleolate as well but the extremely small size of the pseudopuncta of some species makes detection of taleolae very difficult.

"Fine" and "dense" are relative terms. Some measurements of the size of pseudopuncta and the density of packing are presented in the section on histology of the shell. In general, the size of the pseudopuncta is inversely related to the number of pseudopuncta per unit area of shell.

The character of the pseudopuncta of *Maakina, Luhaia,* and *Foliomena* is not known. Contrary to the descriptions of the *Treatise* the pseudopuncta of *Tetraphalerella, Kirkina* and *Macrocoelia* are fine and the pseudopuncta of *Pionomena* are coarse. The size of the pseudopuncta of *Hesperinia* cannot be determined from direct examination and the specimens of this genus are too rare to etch or section. The coarse endospines of the internal surfaces of the valves cause the specimens to appear coarsely pseudopunctate. The closely related *Dactylogonia* bears large endospines but sections reveal fine pseudopuncta.

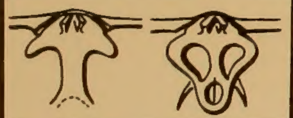
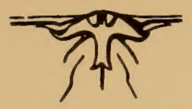
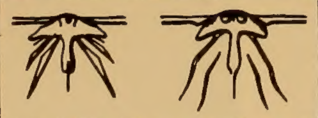
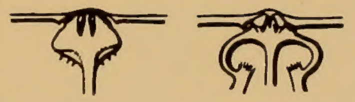
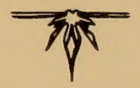
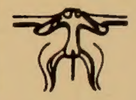
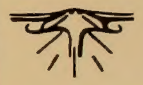
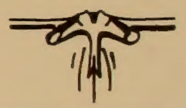
*Shape of the valves.* — The Strophomenacea are fundamentally subrectangular or prolate, slightly alate brachiopods. The earliest genera exhibit pronounced differentiation of shape in the strongly subrectangular form of *Hesperinia* and *Dactylogonia* and the prolate form of *Kirkina.* Inasmuch as most of the genera of the Plectambonitacea are oblate to subrectangular, the prolate form of *Kirkina* probably represents a divergence of shape within the Strophomenacea prior to the known fossil record. The distribution of variations of the shape of the valves within the Strophomenacea is plotted in Text-figure 13.

Shape is not an absolutely consistent feature within each lineage of the Strophomenacea. The Oepikinidae, Rafinesquinidae, Glyptomenini, and Strophomeninae generally are prolate. There are unusual species within each of these lineages which are subrectangular, subtriangular, or oblate. These unusual shapes are regarded as independent divergences from prolate ancestors. Other characteristics indicate that the species with unusual shapes are not anachronistic. The Murinellinae incorporates species without stabilized shape. *Murinella* is oblate to prolate; *Cyphomena* is oblate to subrectangular; *Bellimurina* and *Limbimurina* are prolate. The Leptaenidae in general are strongly subrectangular and alate. Exceptional species of *Leptaena* may be subtriangular or oblate and unusual genera may be prolate, *e.g. Kjerulfina, Bekkeromena* and *Leptagonia.* The Furcitellini and the Teratelasmini are oblate in form.



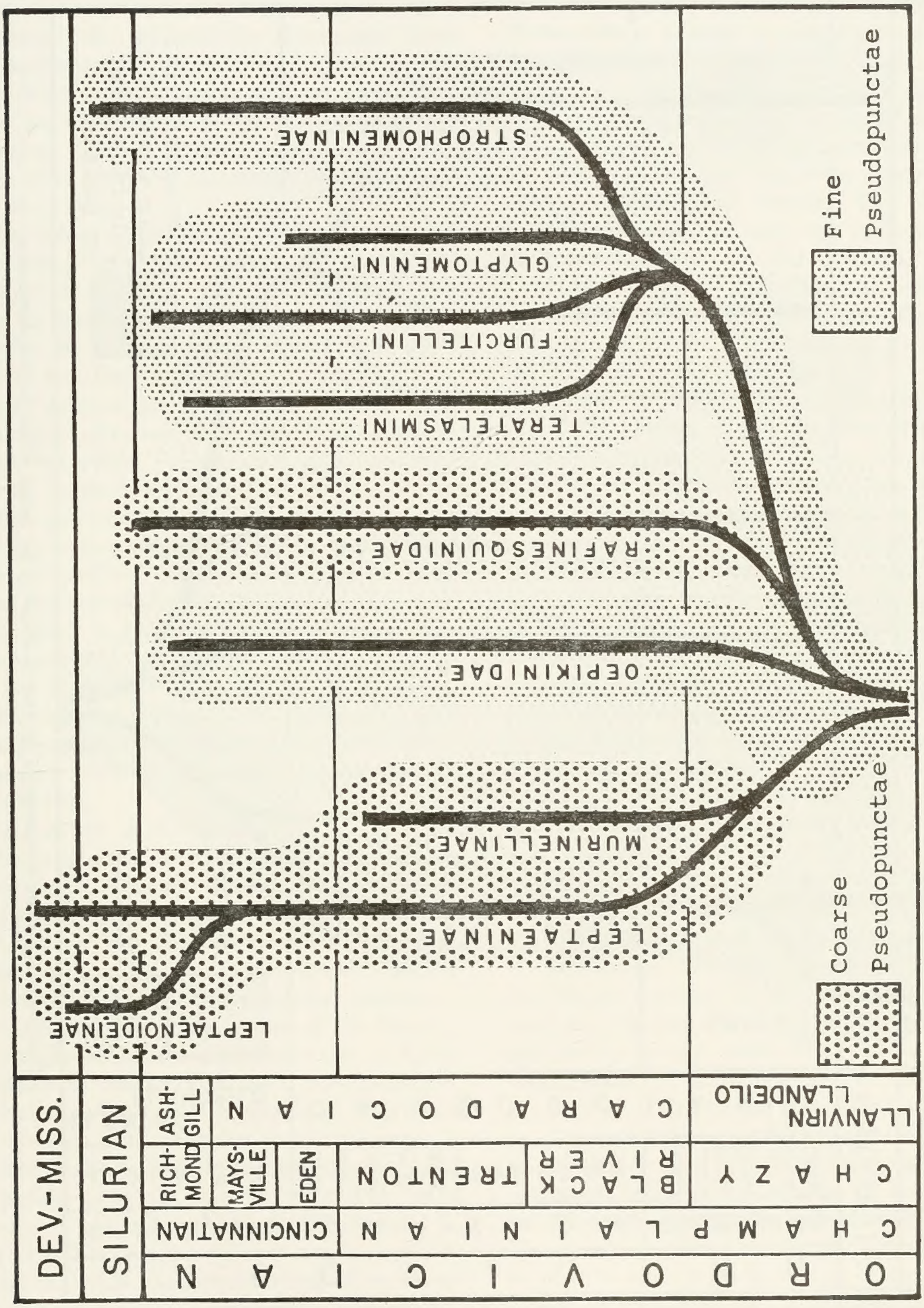
*Text-figure 11.*—The relationship and stratigraphic distribution of genera of the Strophomenidae.

TABLE 1.- SUMMARY OF MORPHOLOGICAL VARIATION IN THE STROPHOMENACEA

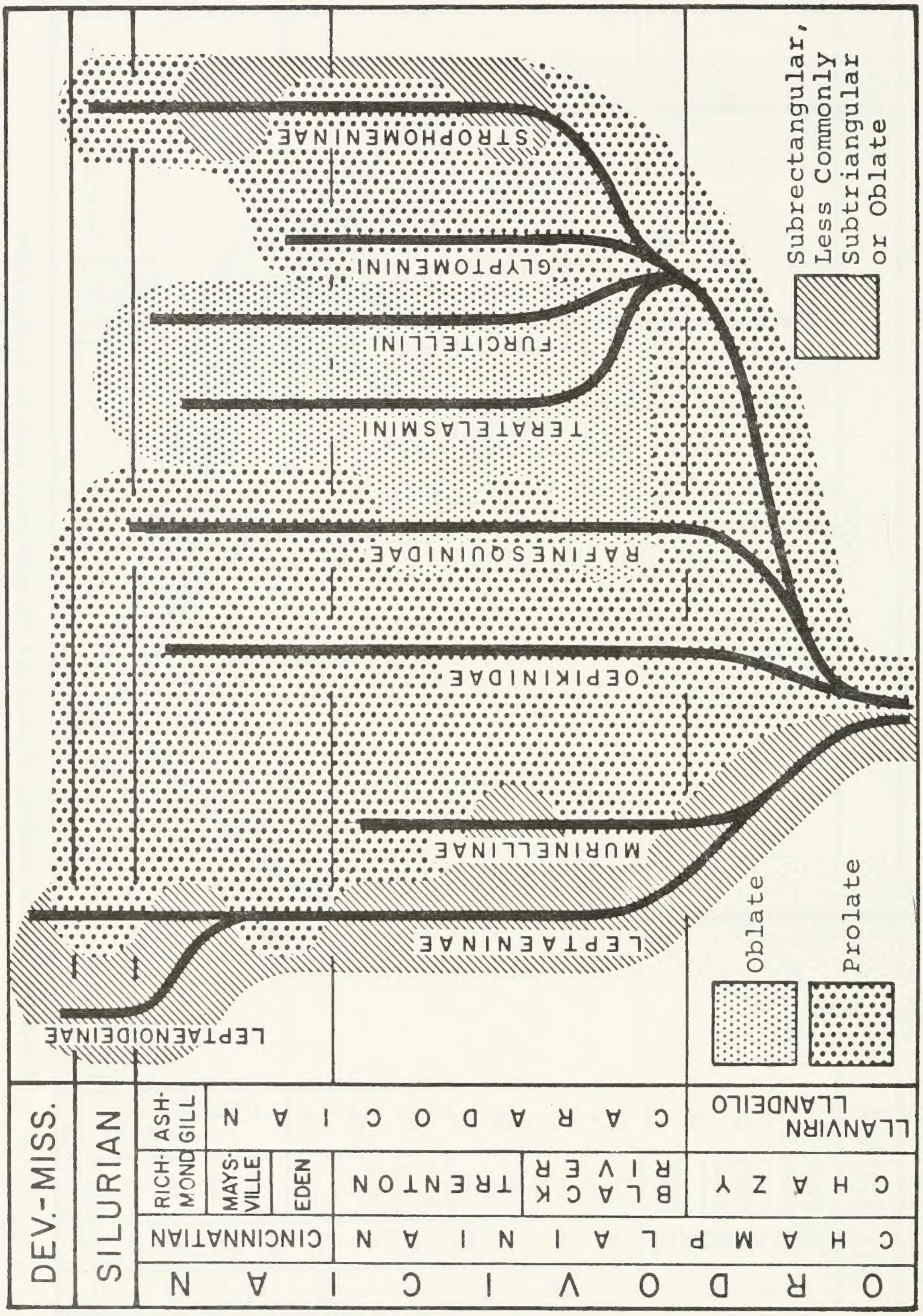
<table>
<tr><td rowspan="3">TAXONOMIC DIFFERENTIA</td><td colspan="2">LEPTAENIDAE</td><td colspan="2" rowspan="3">OEPIKINIDAE</td><td rowspan="3">RAFINESQUINIDAE</td><td colspan="6">STROPHOMENIDAE</td></tr>
<tr><td rowspan="2">LEPTAENINAE</td><td rowspan="2">MURINELLINAE</td><td colspan="5">FURCITELLINAE</td><td rowspan="2">STROPHOMENINAE</td></tr>
<tr><td colspan="2">TERATELASMINI</td><td>FURCITELLINI</td><td colspan="2">GLYPTOMENINI</td></tr>
<tr><td>PSEUDOPUNCTAE</td><td colspan="2">COARSE</td><td colspan="2">FINE</td><td>COARSE</td><td colspan="6">FINE</td></tr>
<tr><td>SHAPE</td><td colspan="2">SUBRECTANGULAR OR SUBTRIANGULAR<br>RARELY OBLATE OR PROLATE</td><td colspan="3">PROLATE<br>ARCHAIC SUBRECTANGULAR |</td><td colspan="3">OBLATE<br>SULCATE | UNIPLICATE</td><td colspan="3">PROLATE</td></tr>
<tr><td>PROFILE</td><td colspan="2">PLANO-CONVEX, CONCAVO-CONVEX, BICONVEX<br>DORSAL, RARELY VENTRAL OR MULTIPLE GENICULATION</td><td colspan="3">CONCAVO-CONVEX<br>ARCHAIC GENICULATION | WEAK DORSAL GENICULATION</td><td colspan="3">BICONVEX<br>CONCAVO-CONVEX |</td><td colspan="2">FLATTENED</td><td>RESUPINATE</td></tr>
<tr><td>DENTAL LAM.</td><td>RECEDING TO ABSENT</td><td colspan="4">COMPLETE</td><td>NONE</td><td colspan="2">COMPLETE TO RECEDING</td><td>NONE</td><td colspan="2">RECEDING, RARELY COMPLETE</td></tr>
<tr><td>TEETH</td><td>DELICATE, POINTED<br>COMMONLY CURVED</td><td colspan="3">LARGE, BLUNT, STRAIGHT<br>ROUNDED ANTERIOR PROJECTION COMMON</td><td>DELICATE, POINTED, STRAIGHT</td><td colspan="2">POINTED<br>CURVED</td><td colspan="3">LARGE, POINTED, STRAIGHT</td><td>LARGE, POINTED TO BLUNT<br>STRAIGHT TO SLI. CURVED</td></tr>
<tr><td>CARDINAL PROCESS</td><td>DISJUNCT BLADES TO CONJUNCT PETALOID BLADES</td><td colspan="2">DISJUNCT BLADES, SHAFTS OR NODES</td><td>HEMICYLINDERS</td><td>DISJUNCT BLADES TO<br>CONJUNCT PETALOID BLADES</td><td colspan="2">POORLY KNOWN</td><td>SHAFTS</td><td colspan="2">MINUTE NODES</td><td>CONJUNCT SHAFTS<br>TO HEMICYLINDERS</td></tr>
<tr><td>MUSCLE BOUND. RIDGES</td><td colspan="3">LATERAL TO COMPLETE<br>COMMONLY LANCEOLATE |</td><td colspan="2">NONE<br>| RARELY LATERAL RIDGES</td><td colspan="5">SHORT LATERAL RIDGES<br>| RARELY LONG |</td><td>GENERALLY COMPLETE RIDGES<br>CIRCULAR</td></tr>
<tr><td>DIDUCTOR MUSCLE SCARS</td><td colspan="3">SMALL, POSTERIOR<br>RARELY LARGE FLABELLATE |</td><td colspan="2">LARGE FLABELLATE<br>| RARELY SMALL</td><td colspan="6">SMALL, POSTERIOR<br>| RARELY LARGE |</td></tr>
<tr><td>SOCKET BUTTRESSES</td><td>STRAIGHT, SHORT, LOW<br>SMALL ANGLE</td><td colspan="2">STRAIGHT TO CURVED, SHORT TO LONG,<br>LOW TO HIGH, LOW TO MEDIUM ANGLE</td><td colspan="2">STRAIGHT, MEDIUM ANGLE<br>SHORT, HIGH | LONG, MEDIUM HIGH</td><td colspan="2">STRAIGHT, HIGH<br>LONG, LARGE ANG.</td><td colspan="4">CURVED, GENERALLY LONG, HIGH<br>MEDIUM TO LARGE ANGLE</td></tr>
<tr><td>POSTERIOR PLATFORM</td><td></td><td></td><td colspan="2"></td><td></td><td colspan="2"></td><td></td><td colspan="2"></td><td></td></tr>
<tr><td>HABIT</td><td colspan="11">LEPTAENOIDEINAE (FAMILY LEPTAENIDAE) CEMENTED BY VENTRAL VALVE TO SUBSTRATE. ALL OTHERS LIVED FREE UPON SEA FLOOR OR TETHERED BY PEDICLE.</td></tr>
</table>

| STRUCTURES WHICH UNDERGO PARALLEL EVOLUTION | | DORSAL RIDGES OR SEPTA | CARDINAL PROCESS | | PSEUDODELTIDIUM | | CHILIDIUM | VENTRAL INTERAREA | PEDICLE FORAMEN | |
|---|---|---|---|---|---|---|---|---|---|---|
| | ADVANCED<br>↑<br>PRIMITIVE | TRUE DORSAL RIDGES OR SEPTA ABSENT<br>↑<br>STRONGLY REDUCED OR MODIFIED RIDGES<br>SLIGHTLY REDUCED OR MODIFIED RIDGES<br>FIVE PROMINENT SEPTA OR RIDGES<br>FIVE PROMINENT STANDING PLATES | LOBES FUSED<br>↑<br>LOBES CONJUNCT<br>LOBES DISJUNCT | LARGE, PETALOID MYOPHORES<br>↑<br>SMALL MYOPHORES | ABSENT<br>↑<br>MINUTE QUOIN<br>SMALL, CONVEX<br>LARGE, CONVEX | PEDICLE CALLIST<br>↗ | LARGE<br>↑<br>SMALL | NARROW<br>↑<br>WIDE | SEALED<br>↑<br>SMALL<br>LARGE | DELTHYRIAL APERTURE WITH PEDICLE CALLIST<br>↗ |

| | | | | | |
|---|---|---|---|---|---|
| FEATURES OF LITTLE SIGNIFICANCE | SIZE.- NOT TAXONOMICALLY DISTINCTIVE. GENERAL INCREASE FROM OLDER TO YOUNGER GENERA WITH MANY EXCEPTIONS. | PROSOPON.- NOT DISTINCTIVE FOR FAMILY RANK TAXA. MUCH HOMEOMORPHY. NO EVOLUTIONARY TRENDS. | ADDUCTOR MUSCLE SCARS.- POSITION AND SIZE NOT TAXONOMICALLY DISTINCTIVE. NO EVOLUTIONARY TREND OBSERVED. | MESO-CARDINAL RIDGE.- A GERONTIC STRUCTURE. NO EVOLUTIONARY OR TAXONOMIC SIGNIFICANCE. | VASCULAR MARKINGS.- TOO OBSCURE TO BE EVALUATED. |



*Text-figure 12.*—The distribution of coarse and fine pseudopuncta within the Strophomenacea.



*Text-figure 13.*— The distribution of the various shapes of the valves within the Strophomenacea.

There seems to be an association of the subrectangular and oblate shapes with geniculation. Commonly these characters are accompanied by concentric rugation of the valves. If there is an interrelationship of these characters, the independent character cannot be distinguished from the dependent characters. Neither subrectangular shape, geniculation or rugae occur always in association with either of the other two characters.

*Profile of the valves.* — The Strophomenacea are fundamentally plano-convex or slightly concavo-convex brachiopods. Text-figure 14 illustrates the distribution of the various profiles of the valves and shapes of the anterior commissure within the Strophomenacea. The earliest oepikinids, *Hesperinia* and *Dactylogonia,* have basically plano-convex or faintly concavo-convex profiles with a dorsally geniculated short trail. *Kirkina* has a weakly concavo-convex, smoothly curved profile. The basic profile of *Hesperinia* and *Dactylogonia* persists throughout the history of the Leptaeninae. The only general modification which occurs in this subfamily involves lengthening of the trail. Exceptions to the general profile of the Leptaeninae are found in *Kiaeromena* and *Bekkeromena* which are not sharply geniculate, *Kjerulfina* which is ventrally geniculate and *Leptagonia* which is biconvex.

There is no consistent profile in the Murinellinae. *Murinella* is biconvex or plano-convex. *Cyphomena* and *Bellimurina* are plano-convex or concavo-convex with short, dorsally geniculated trails. The multiple geniculation of *Limbimurina* is unique.

The younger genera of the Oepikinidae, the Rafinesquinidae and the Strophomenidae have smoothly curved profiles. Sharp geniculation as found in the Leptaenidae is rare. Weak geniculation is relatively common among the younger species of each family. The Oepikinidae and the Rafinesquinidae are composed entirely of concavo-convex species. The Strophomenidae begins with the weakly resupinate, weakly concavo-convex or biplanate genera of the Glyptomenini. The strongly resupinate Strophomeninae and the biconvex, uniplicate or sulcate Furcitellini and Teratelasmini diverge from the flattened Glyptomenini. Only concavo-convex *Foliomena* is an exception to this sequence.

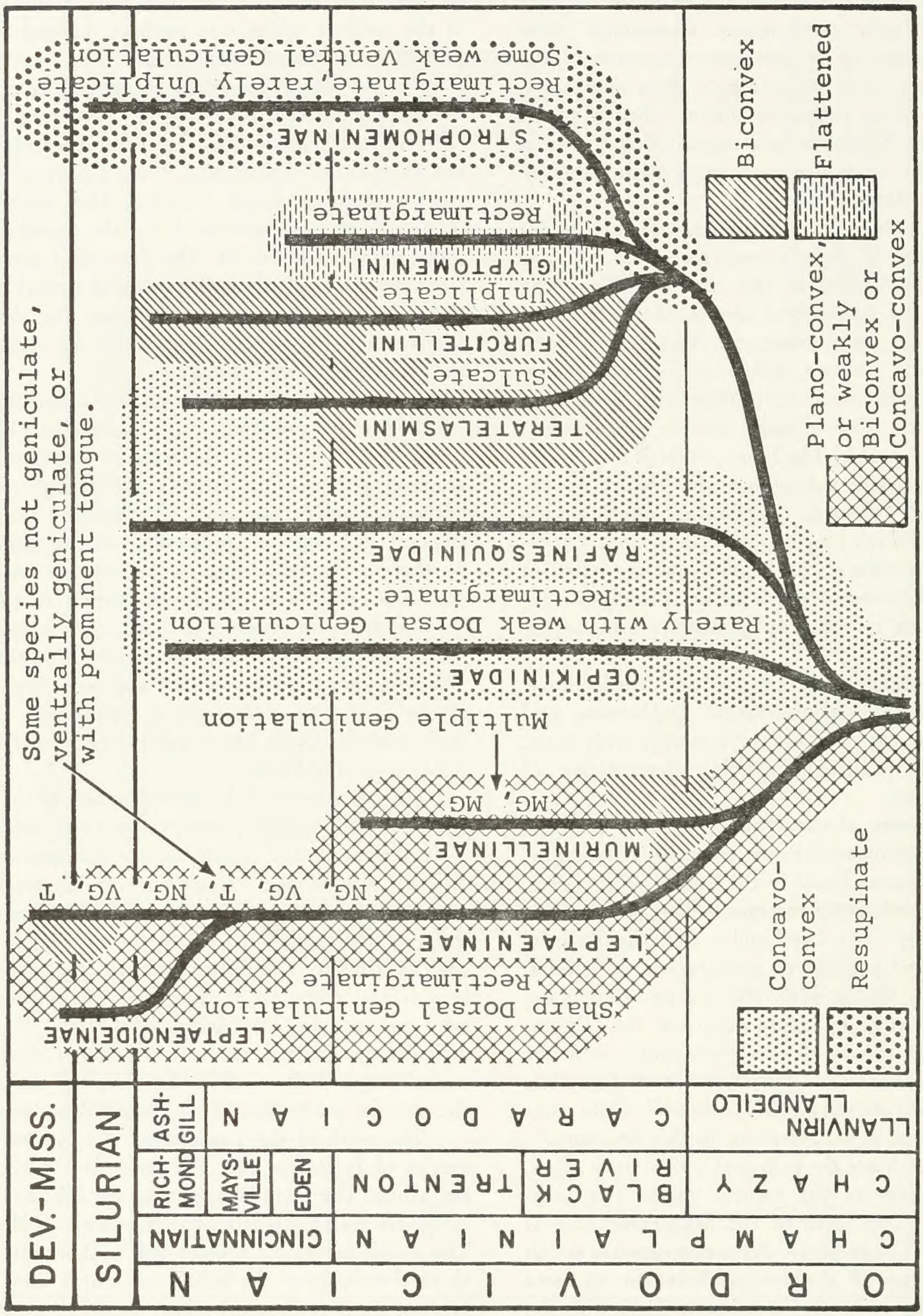
***Teeth.*** — The teeth are the principal articulatory edges, surfaces and projections of the ventral valve. The taxonomic significance of the teeth of the Strophomenacea is difficult to evaluate. The teeth are delicate structures which project into the cavity of the ventral valve in, or even slightly dorsal to, the plane of commissure. Consequently, it is unusual to find teeth preserved without abrasion or fracture. Moreover, the taxonomic significance of variations of the teeth is difficult to evaluate because the variations probably are related to the profile of the valves and to the form of the dental lamellae. The character of the teeth of the Strophomenacea is plotted in Text-figure 15.

The teeth are formed by confluence of the shell tissue along the delthyrial edge of the palintrope with the narrow or receding dental lamellae. This angular confluence of shell tissue is penetrated by the cuneiform denticular plate, see Text-figure 25. The denticular plate is emergent from the tissue of the palintrope and dental lamellae along the dorsal margin of the delthyrium. The denticular plate projects a short distance anterior to the anterior edge, *i.e.* the free edge, of the palintrope.

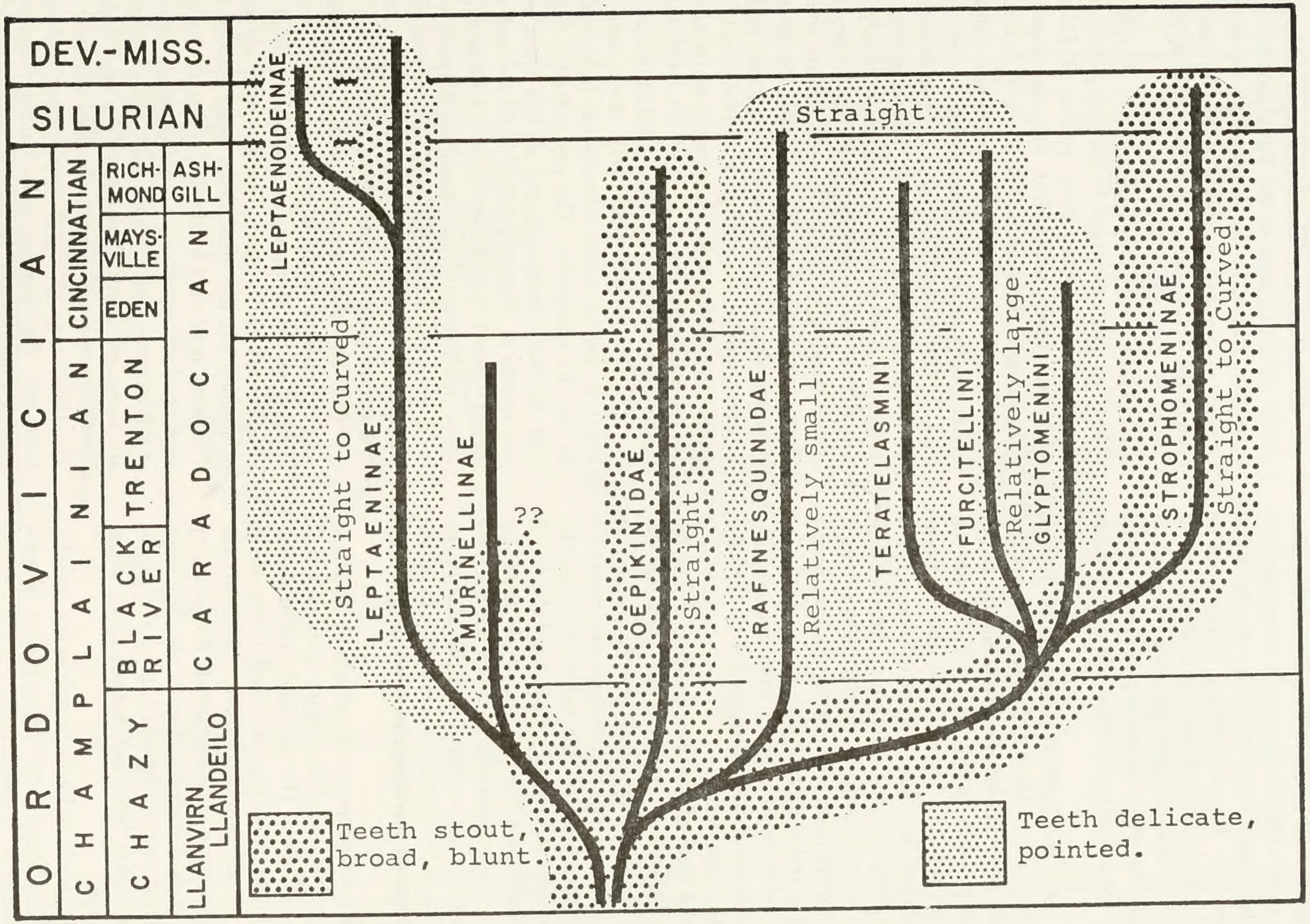
The teeth of the oepikinids are relatively stout structures. The anterior end of the denticular plate is broadly rounded. Judging from the sites of semidenticulation and abrasion, the principal articulatory contact with the socket buttress occurs on the medial surface and the medial-dorsal edge of the anterior projection of the denticular plate. Neither the dorsal surface of the anterior projection of the denticular plate nor the dorsal margin of the delthyrium show pronounced evidence of articulatory contact. The teeth of the Oepikinidae, Strophomeninae, *Murinella,* and *Rhipidomena* are similar in shape and in abrupt demarkation of the denticular plate from the palintrope on the dorsal surface of the tooth. Details of the teeth of *Hesperinia* and *Kirkina* are not known.

Only *Murinella* of the several genera of the Murinellinae has teeth well enough preserved for some detailed examination. Unfortunately, many of the specimens are silicified and the size of the irregularities of silicification approximately equal the size of semidenticles. The general size and shape of the teeth of *Murinella* correspond to the teeth of the Oepikinidae. The dental lamellae of *Murinella* are flared in a lateral direction at their base. As a result, the teeth tend to overhang the delthyrial cavity. The surfaces of articulatory contact seem to be under the overhanging medial edges of the teeth and on the flat dorsal surfaces of the anterior projections of the denticular plates.

The teeth of the Leptaeninae are curious structures if species of *Leptaena* and *Megamyonia* are adequate representatives. The teeth of *Leptaena* are delicate. The denticular plates are emergent along the margin of the delthyrium. The denticular plates project only a short distance anterior to the free edge of the palintrope where they terminate in narrow, sharp points, not blunt knobs as in *Oepikina.* The dental lamellae of *Leptaena* are receding or obsolescent. The



*Text-figure 14.*— The distribution of the various profiles of the valves and shapes of the anterior commissure in the Strophomenacea.



*Text-figure 15.*— The shape of the teeth of the Strophomenacea.

poorly supported teeth tend to curve in a lateral direction. Curvature of the teeth also is observed in some strophomenids and may be related to obsolescence of the dental lamellae in both families. The articulatory surfaces are on the ventral sides, *i.e.* undersides, of the denticular plates of *Leptaena.* The teeth of *Megamyonia* resemble the teeth of *Oepikina* except that the teeth are not supported on dental lamellae. Details of the articulatory surfaces of *Megamyonia* are not known.

The teeth of the Rafinesquinidae tend to be delicate and sharply pointed as the teeth of *Leptaena.* The teeth of the rafinesquinids do not resemble the stout, bluntly terminated teeth of the oepikinids. Unlike the teeth of *Leptaena,* the teeth of the Rafinesquinidae are straight and are borne on thin, vertical dental lamellae. The denticular plate is emergent along the margin of the delthyrium. The denticular plate projects as a short, sharp or angular point from the anterior edge of the palintrope. Articulatory contact occurs on the medial surface and delthyrial edge of the denticular plate. There is no evidence to indicate extensive articulatory contact on the dorsal or ventral surface of the anterior projection of the denticular plate.

The shape of the teeth of the Furcitellinae, except for *Rhipidomena* and *Foliomena,* resemble the teeth of the Rafinesquinidae by being straight and sharply pointed at the anterior. The teeth of the Furcitellinae are relatively larger in proportion to the size of the valves than are the teeth of the Rafinesquinidae. Both the medial and the dorsal surfaces of the anterior projection of the tooth serve for articulatory contact in the furcitellines. Only *Teratelasma* shows evidence of articulatory contact along the edge of the delthyrium. The teeth of *Foliomena* are not known in detail. The teeth of *Rhipidomena* resemble the teeth of the Strophomeninae.

The teeth of the Strophomeninae are similar in shape to the teeth of the Oepikinidae. The anterior terminations of the teeth are broad and blunt. The principal sites of articulatory contact are the dorsal surface and medial edge of the anterior projection of the denticular plate. As noted, the teeth of the Strophomeninae may be curved. An accessory socket commonly is formed in the surface of the palintrope on the posterior-lateral side of the tooth of the Strophomeninae. The lateral socket buttress functions as an accessory tooth in this family.

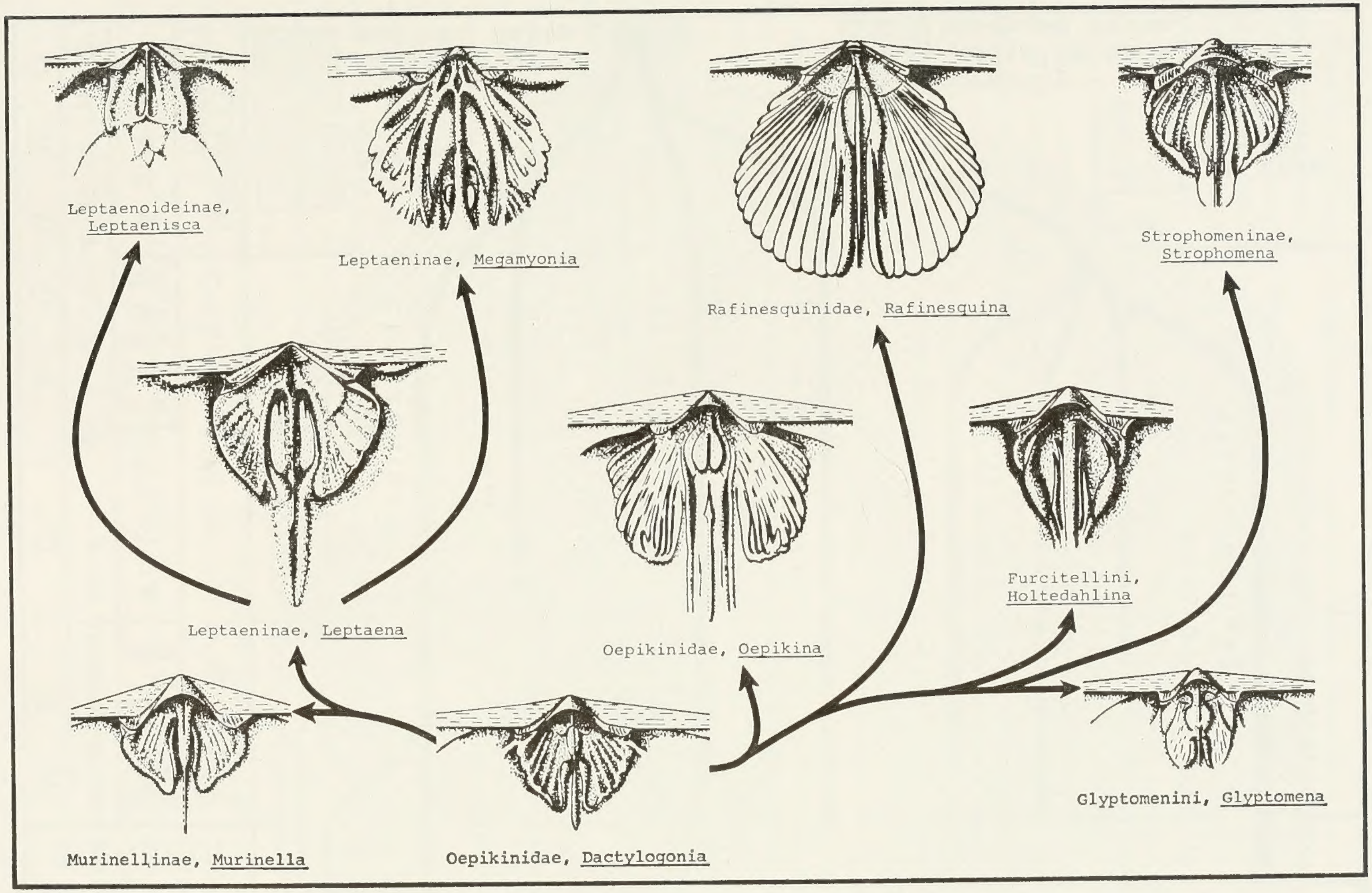
The shape of the teeth, diductor muscle scars, pseudodeltidium and delthyrial cavity of several genera of strophomenaceans illustrated in Text-figure 16.

*Dorsal septa.* — The dorsal septa undergo parallel evolution in the lineages of the Strophomenacea. Four distinct evolution stages, *i.e.* isophenes, may be defined in the sequence of gradual reduction or modification and eventual loss of the dorsal septa. The distribution of the four stages is shown in Text-figure 17.

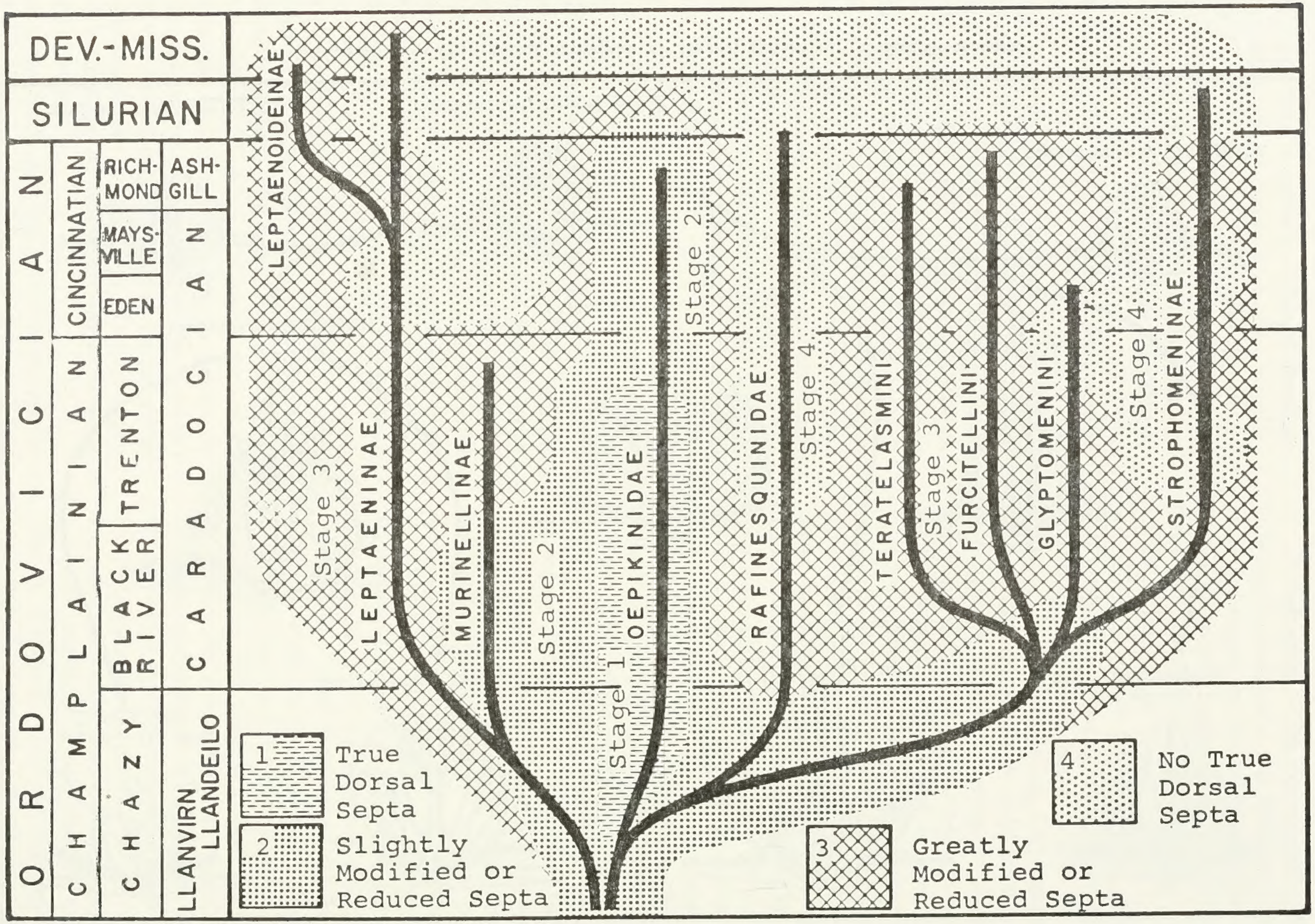
(1) The septa may be long, high, sharply defined ridges which are not submerged in secondary shell tissue or interrupted by endospines. Some species of *Dactylogonia* and *Oepikina* possess unmodified, fully developed dorsal septa. For example, the specimen of *O. formosa* Cooper shown in Text-figure 4, number 6, belongs in this category. Possibly those species of *Dactylogonia* which possess standing plates, *e.g. D. geniculata* Ulrich and Cooper, deserve a separate category preceding this one. The standing plates of *D. geniculata* and related species more closely resemble the septa of the plectambonitaceans than the septa of *Oepikina.* These standing plates are not duplicated elsewhere among the strophomenaceans. Thus, it is not known at this time if these standing plates belong to a separate evolutionary stage or are a unique innovation of *Dactylogonia.* The plectambonitacean character of the standing plates of *Dactylogonia,* among other characters, support the belief that this genus is the most archaic, but not the oldest, strophomenacean.

(2) The dorsal septa may show some reduction of length or height, slight submergence in secondary tissue or overlap by endospines. The septa in this second category may be easily recognized and all five septa are present. A few species of *Oepikina* which have reduced septa, *e.g. O. bellula* Cooper, and *Dactylogonia incrassata* (Hall) which shows interference of the septa by endospines may be placed in this second stage. *Kirkina, Macrocoelia, Rhipidomena, Hesperinia, Murinella, Cyphomena,* and *Maakina* belong in this second stage of septal development.

(3) The third stage of septal development includes species in which the dorsal septa are short, low or indistinct, or in which the septa are extensively modified by additions of secondary shell tissue or conflict with adventitious septa. Commonly the five true dorsal septa cannot be identified. The most persistent of the five septa is the medial dorsal septum which appears as a breviseptum in almost all genera of this category and category four. The anterior dorsal septa are more commonly absent than the medial dorsal septum but more commonly present than the posterior dorsal septa. The third stage of septal development includes species of *Leptaena, Kiaeromena,* questionably *Leptaenisca, Bellimurina, Limbimurina, Oslomena,* questionably *Colaptomena,*



*Text-figure 16.*—The ventral cardinalia of several genera of the Strophomenacea.



*Text-figure 17.*—The stages of development of the dorsal septa of the Strophomenacea. The division of the Leptaenidae, Oepikinidae, and Strophomenidae into stages is not related to any specific epoch.

*Glyptomena, Platymena, Actinomena, Furcitella, Holtedahlina, Teratelasma, Foliomena, Microtrypa, Trigrammaria, Pentlandina,* and species of *Strophomena.*

(4) The final stage is defined by the absence of the posterior and anterior pairs of dorsal septa. The medial dorsal septum or breviseptum generally is present in the species of the fourth category. This final stage of the parallel evolution of the septa includes most of the species of *Leptaena, Kjerulfina, Megamyonia, Bekkeromena, Leptagonia, Leptaenella, Notoleptaena, Rafinesquina, Kjaerina, Hedstroemina, Mjoesina, Longvillia, Gunnarella, Tetraphalerella* and some of the species of *Strophomena.* The stage of septal development of *Luhaia, Pionomena, Leptaenoidea,* and *Rugoleptaena* is not known.

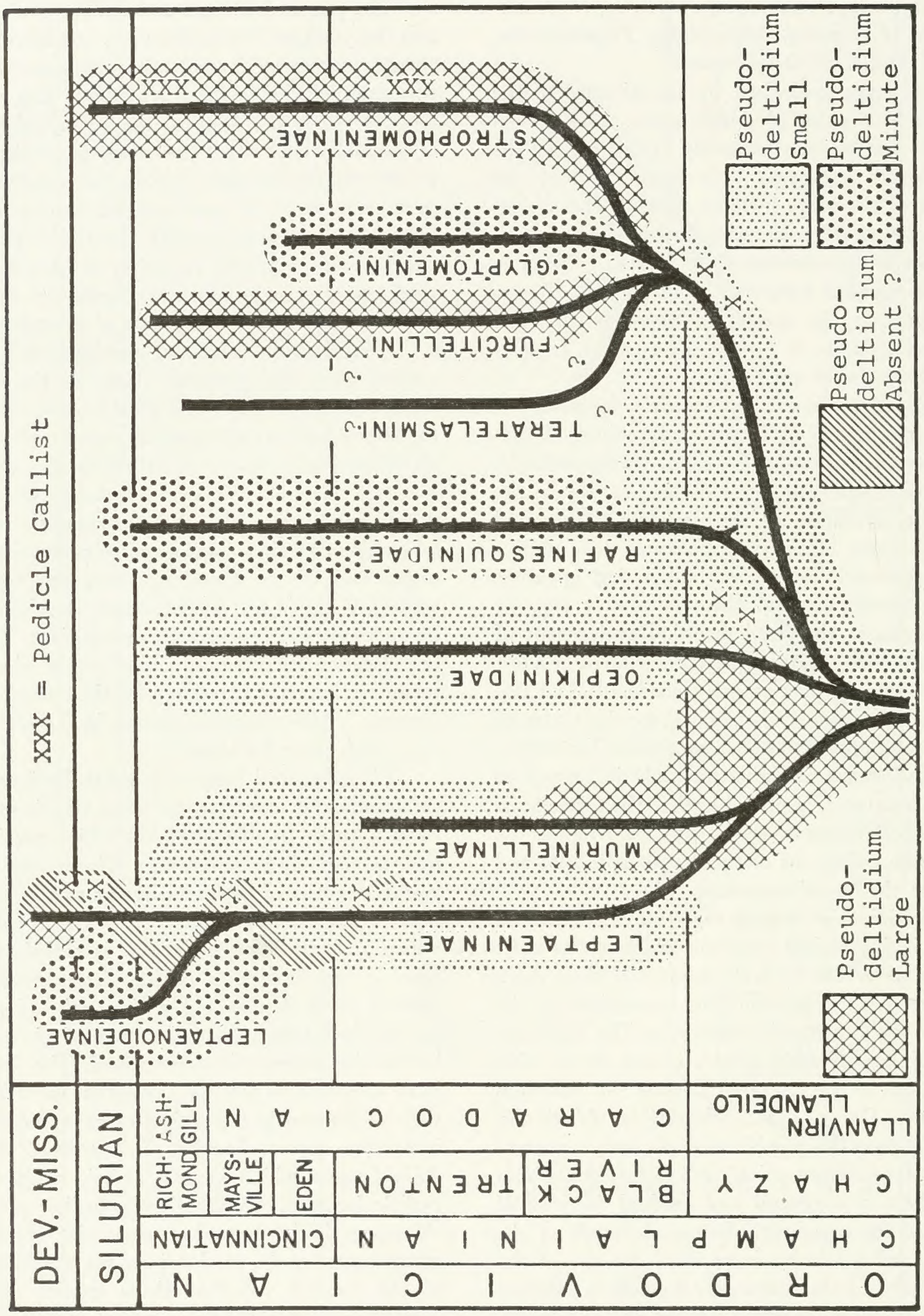
*Pseudodeltidium, chilidium and pedicle foramen.* — The comparative morphology of the pseudodeltidium, chilidium, and pedicle foramen cannot be considered independently. Distinct isophenous stages cannot be defined readily in the progressive parallel evolution of the pseudodeltidium and chilidium of the lineages of the Strophomenacea. Modification of these two structures form a continuum. Any apparent discontinuities in development of these structures may be related to deficiencies in the fossil record. Development of the pedicle foramen does progress through isophenes if adult individuals of the various species are considered. The isophenes of the pedicle foramen are defined by the states of being open and large, open and small, or sealed. The condition of the pedicle foramen is significant only in respect to adult individuals because it is probable that the foramen of all juvenile strophomenaceans was open. Text-figures 18 and 19 illustrate the conditions of the pseudodeltidium and pedicle foramen in the Strophomenacea.

The pseudodeltidium of several early strophomenacean genera is a large, highly arched structure which covers most of the delthyrial cavity. The ventral interarea of these early genera is long (posterior to anterior) in comparison to the ventral interareas of other strophomenaceans. The large size of the pseudodeltidium of early genera is not attributable entirely to the length of the interarea because the chilidium is relatively short. *Dactylogonia, Hesperinia, Murinella,* and *Cyphomena* possess this combination of posterior structures as well as a large, supra-apical pedicle foramen. From this beginning, there is a general and gradual decrease of the relative size of the pseudodeltidium and length of the ventral interarea, and a relative increase of the size of the chilidium. Accompanying these changes, the pedicle foramen of adult strophomenaceans becomes smaller and eventually is sealed by secondary shell tissue.

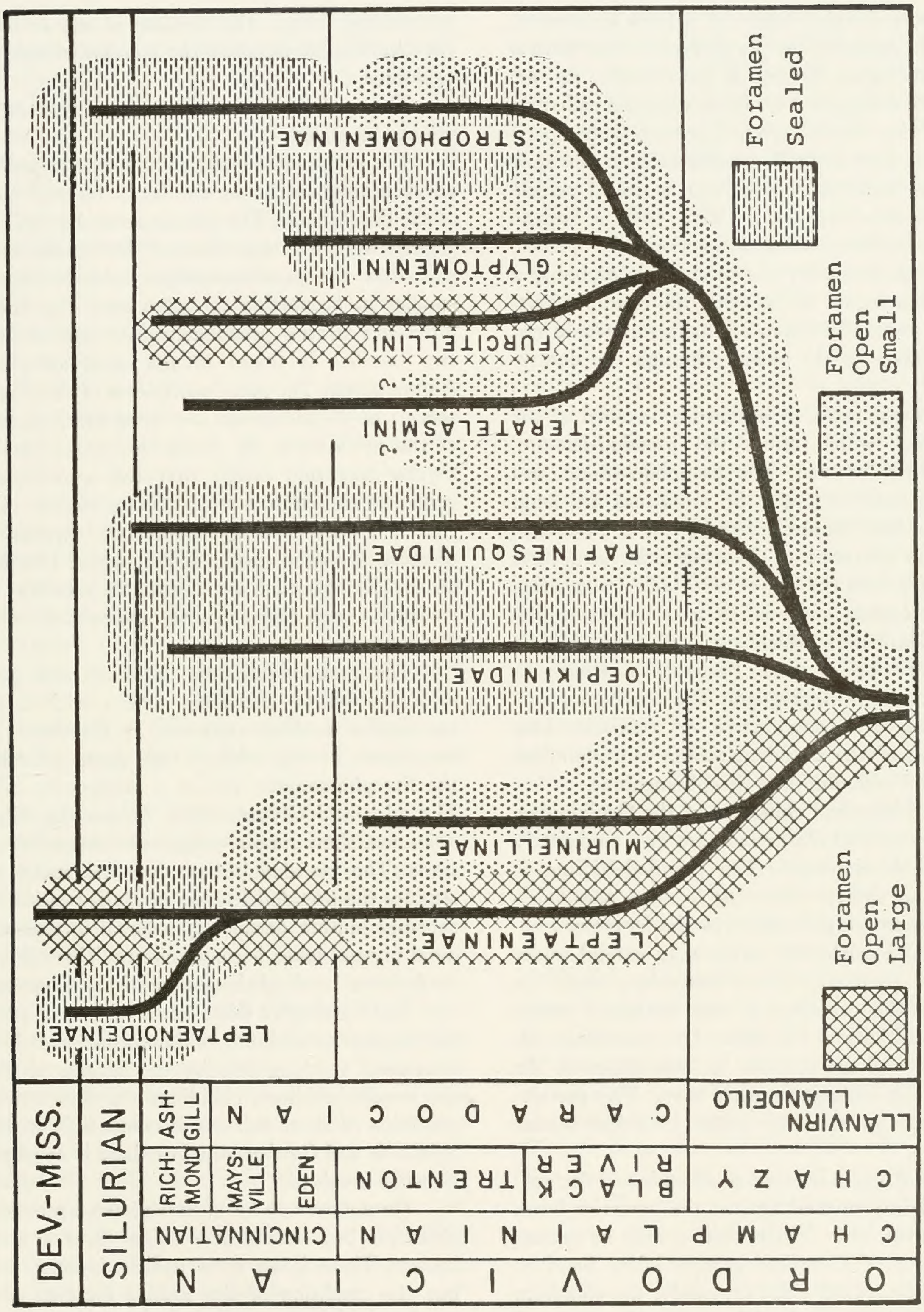
The pseudodeltidium and chilidium of the Leptaeninae and the younger Murinellinae are considerably smaller than these structures of the older strophomenaceans. The pseudodeltidium of the younger leptaenids is a small pyramidal block set into the apex of the delthyrial cavity. Deposits of secondary shell tissue commonly cover the anterior surface of the pseudodeltidium within the delthyrial cavity. The pseudodeltidium of some species cannot be distinguished from the surrounding shell tissue. In particular, species which possess a pedicle callist rarely have a pseudodeltidium that can be recognized on the surface of the shell.

The chilidium of all species of the younger leptaenids is a distinct but thin sheet of wrinkled shell tissue which is molded onto the posterior bases of the cardinal process lobes. A large chamber may exist between the chilidium and the lateral bases of the cardinal process lobes. A similar condition is found in species of *Oepikina.* The chilidium is either fused to the posterior edge of the meso-cardinal ridge or deeply folded into the cleft between the cardinal process lobes. The chilidium appears to be protrusive because of the narrowness of the dorsal interarea and because, in many species, there is not an emergent pseudodeltidium but an introverted pedicle callist for comparison. The small size of the pseudodeltidium and chilidium of the advanced leptaenids is directly correlated to their exceedingly short interareas. These structures cannot be larger; there would not be enough room for them.

The advanced leptaenids generally have an open pedicle foramen in contrast to other strophomenaceans which have a small pseudodeltidium. Older species of *Leptaena* have a relatively large foramen. *Kiaeromena* and some of the younger species of *Leptaena* have a small foramen. The foramen of *Megamyonia,* some species of *Leptaena, Bekkeromena,* and the Leptaenoideinae is sealed. The pedicle foramen of the leptaenids lies on the external surface of the ventral valve. Commonly a thin yoke of shell tissue separates the foramen from the apex of the pseudodeltidium, hence, the foramen is supra-apical. The foramen seems to have increased in size by resorption of shell tissue because the rim commonly is polished or calloused and the foramen interrupts costae. Species of *Leptaena, Macrocoelia* and *Rhipidomena* which have a pedicle callist do not have a pedicle foramen. Apparently the pedicle protruded through the open delthyrium. A curious slot commonly is found which seems to be eroded into the posterior-medial region of the ventral valve of those species of *Leptaena* and *Rhipidomena* which have a pedicle callist. Apparently, the pedicle passed through the open delthyrium, curved over



*Text-figure 18.*—The approximate size of the pseudodeltidium of strophomenaceans relative to the general size of the valves.



*Text-figure 19.*—The condition of the pedicle foramen in adult strophomenaceans.

the apex of the ventral valve where it left no impression, and abraded or was cemented to the midline of the ventral valve anterior to the apex. Species of *Macrocoelia, e.g. M. expansa* (J. de C. Sowerby), which have a pedicle callist do not have a slot in the ventral valve. However, some specimens of *Macrocoelia* have a small, circular facet at the apex of the ventral valve which may have been a site of pedicle attachment. *Leptagonia* appears to have both a pedicle callist and an open foramen on first inspection. The "pedicle callist" of *Leptagonia* is smooth and thick. It is probably a filling of the posterior region of the delthyrial chamber inasmuch as the large pseudodeltidium of this genus would not have permitted passage of the pedicle through the delthyrium.

*Leptagonia* demonstrates an interesting reversal of the evolutionary changes which effect the pseudodeltidium, chilidium and pedicle foramen. The pseudodeltidium and chilidium of this genus are large; the interareas are long; there is an open pedicle foramen. *Leptagonia* is Mississippian in age, yet the character of these posterior structures belong to a leptaenid from the Lower or Middle Ordovician. It is not likely that *Leptagonia* arose from an unknown lineage of primitive leptaenids which survived from Middle Ordovician to Mississippian time. Probably *Leptaena* or *Leptaenella* is ancestral to *Leptagonia*. The posterior structures of *Leptagonia* are conservative or atavistic. Less pronounced atavism of the pseudodeltidium and chilidium is found also in the Furcitellini and Strophomeninae.

The pseudodeltidium and chilidium of the Oepikinidae, excluding *Dactylogonia* and *Hesperinia,* are in a moderately advanced state of development. The pseudodeltidium is smaller, thicker, and shorter than the archaic pseudodeltidium. It is not a pyramidal block as in the leptaenids because the apex of the delthyrial cavity may extend under the slightly arched pseudodeltidium. Secondary shell tissue commonly fills the extension of the delthyrial cavity under the pseudodeltidium of *Oepikina*. This secondary tissue is drawn-out toward the anterior to form ridges on the lateral margins of the adductor muscle scars. The pseudodeltidium is replaced by a pedicle callist in a few species of *Macrocoelia*.

The chilidium of the advanced oepikinids is relatively large. It may be tightly pressed against the posterior bases of the cardinal process lobes. The chilidium may be draped into the cleft between the cardinal process lobes, fused to the edge of the meso-cardinal ridge or, rarely, the chilidium may bridge the cleft between the lobes to produce a small notothyrial cavity. The increase of size of the chilidium in the Oepikinidae parallels the increase of size in the Rafinesquinidae.

The pedicle foramen of the advanced oepikinids is minute or sealed.

The pseudodeltidium, chilidium, and pedicle foramen of the Rafinesquinidae are similar in form to those structures of the Oepikinidae. The interareas of the Rafinesquinidae are slightly narrower than those of the Oepikinidae with the result that the pseudodeltidium and chilidium are slightly smaller in proportion to valve size. The only outstanding difference in the pseudodeltidium and chilidium of these two families is found in the most advanced species of *Rafinesquina*. The pseudodeltidium of the Upper Ordovician species of *Rafinesquina* is a very small quoin in the apex of the delthyrium. In detail, the quoin has the form of a regular trapezoid except that the opposite sides are concave arcs rather than straight parallel lines. The pseudodeltidium is buttressed by a secondary deposit. The chilidium of these advanced species is very large. The pedicle foramen of the Rafinesquinidae is minute, possibly open in *Hedstroemina* and *Colaptomena,* and sealed in *Kjaerina* and *Rafinesquina*.

The pseudodeltidium, chilidium and pedicle foramen of *Rhipidomena,* excepting species with a pedicle callist, are similar to these structures in *Oepikina*. That is, these structures in the oldest and most primitive genus of the Strophomenidae are in a moderately advanced state. The advanced Glyptomenini, *Platymena, Glyptomena* and *Mjoesina,* show simple, progressive reduction of these structures. The pseudodeltidium becomes small so that it resembles the pseudodeltidium of *Rafinesquina*. The chilidium becomes minute because the dorsal interarea and the cardinal process lobes become minute. There is a minute pedicle foramen in all of the genera of the Glyptomenini.

The Furcitellini show conservatism, or perhaps atavism, of the pseudodeltidium, chilidium and pedicle foramen. The interareas are long relative to the size of the valves and the pseudodeltidium, chilidium and foramen are large. The condition of these features is compatible with that of *Dactylogonia* and *Cyphomena,* but there is no phylogenetic relationship involved.

*Teratelasma* and *Foliomena* have a pseudodeltidium and chilidium but details concerning these structures are not known. There is an open pedicle foramen in *Teratelasma* but the condition of the pedicle foramen of *Foliomena* is not known.

The Strophomeninae also shows conservatism or atavism of the pseudodeltidium and chilidium. The ventral interarea of species in this subfamily is moderately long. The pseudodeltidium is long and highly arched. Unlike other genera which have a large pseudodeltidium, most of the species of *Strophomena* and allied genera have a sealed foramen. The chilidium is relatively small. It adheres to the posterior and lateral bases of the cardinal process lobes. A meso-cardinal ridge is rarely present in the strophomenids. The meso-cardinal ridge, if present, lies on the posterior-medial base of the cardinal process under the chilidium. As a consequence, well-preserved specimens of strophomenids have a distinct notothyrial cavity.

No measurements have been taken of dental angles throughout the Strophomenacea. The dental angle is the angular divergence of the edges of the delthyrium in the plane of the interarea. Bancroft (1929) showed that the dental angle of species of *Kjaerina* and *Hedstroemina* is variable. Moreover, the dental angle is not constant throughout the ontogeny of those species with curved teeth, *e.g.* species of *Leptaena* and *Strophomena*. The general appearance of the dental angle of the various genera suggests that the dental angle is inversely related to the length of the interarea and to the size of the pseudodeltidium. The shorter the interarea and the smaller the pseudodeltidium, the greater is the dental angle. This relationship seems plausable in respect to the mechanics of the cardinal process and articulation.

*Cardinal process.* — The form of the cardinal process and the shape of the cardinal process lobes are highly variable qualities in the Strophomenacea. The cardinal process in general and the lobes in particular show little in the way of orderly evolutionary progression or taxonomic differentiation. It is probable that the poor organization of these structures in respect to evolutionary progression and taxonomic differentiation is caused by the interplay of at least four independent variables. These are, taxonomic lineage, evolutionary stage of development within each linage, the ontogenetic stage of individuals examined and the effects of weathering, natural abrasion and preparation upon the individuals examined. If perfectly preserved individuals of the same ontogenetic stage were available for all genera, probably a more meaningful and orderly arrangement of cardinal process types could be found. Text-figure 20 shows sketches of the dorsal cardinalia of selected strophomenacean genera. The cardinal processes are shown.

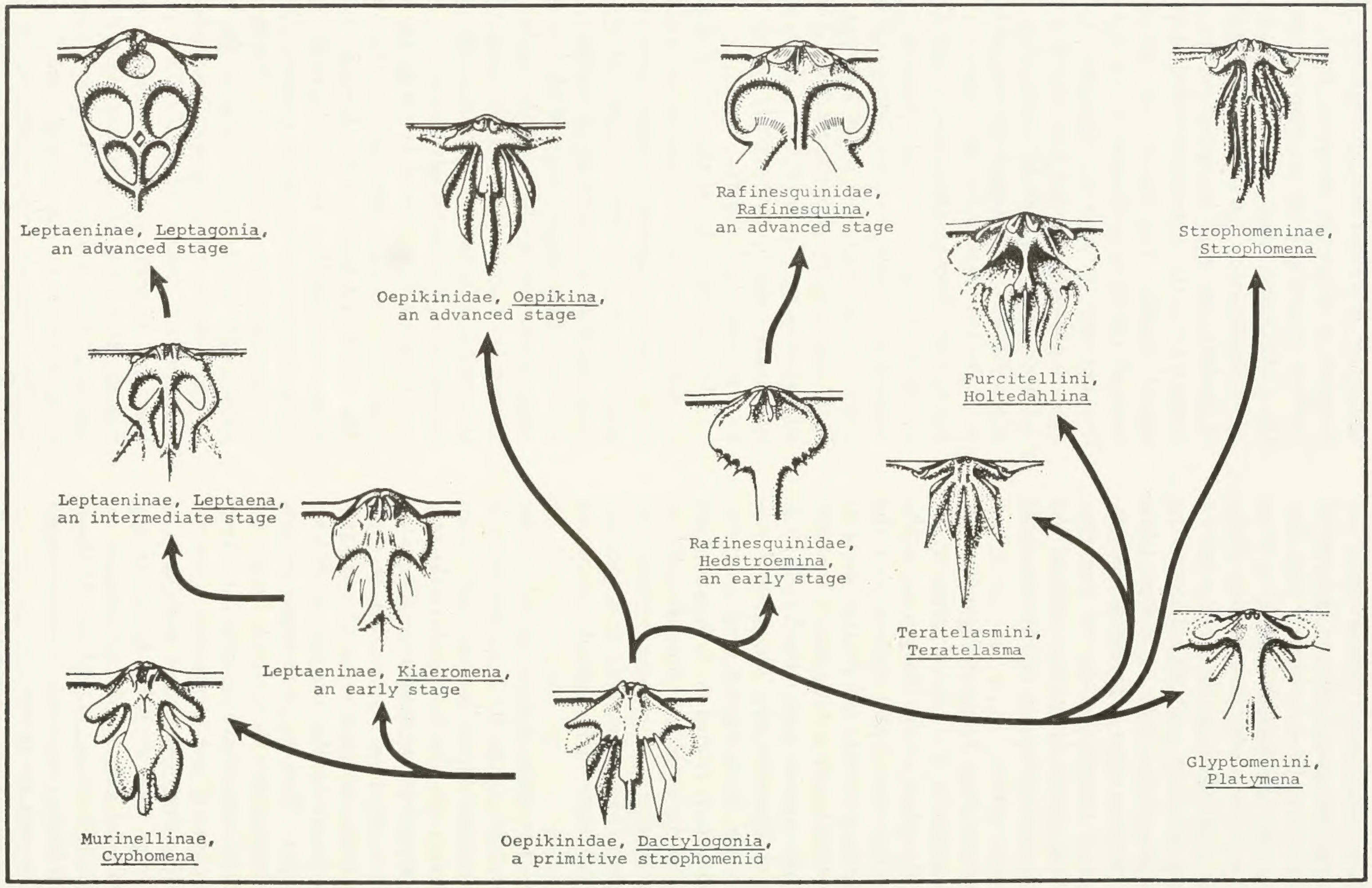
The cardinal process lobes show some slight taxonomic differentiation in the shape of the base of the lobes, the amount of space between the bases of the lobes and the direction in which the myophore faces. Unfortunately, the cardinal processes of the oldest strophomenaceans, *Hesperinia* and *Kirkina,* which are rare, are too abraded to yield much information. The bases of the cardinal process lobes of *Kirkina* are small in respect to the size of the valve, elongated in the anterior-posterior direction and closely spaced together. The narrow cleft has parallel sides. The bases of the lobes of *Hesperinia* are like those of *Kirkina* but are larger in respect to the size of the valves. Specimens of *Dactylogonia* and *Cyphomena* are better preserved and more numerous than *Hesperinia* and *Kirkina.* The form of the bases of the lobes of *Dactylogonia* and *Cyphomena* resembles the bases of the older genera. The distal terminations of the lobes of *Dactylogonia* and *Cyphomena* are irregular knobs or shafts with narrowly cupped myophores directed toward the posterior. Some individuals of *Dactylogonia* have a small fillet added between the anterior base of the lobe and the posterior platform. The archaic cardinal process lobes may be described as shafts or irregular knobs, with posteriorly directed myophores, elongate bases and a narrow, parallel sided cleft.

The parallel sides of the cleft of these archaic genera, as well as the older Leptaeninae and Rafinesquinidae, would seem to indicate a disjunct condition of the cardinal process lobes. The posterior ends of the cardinal process lobes of advanced genera of all lineages tend to merge together, *i.e.* they become conjunct. It is strange that the disjunct to conjunct evolution of the cardinal process and the relative increase of size and importance of the chilidium of the Strophomenacea are opposite to the evolution of these structures in the Stropheodontacea.

The cardinal process of *Murinella* has approximately the same shape as that described for the other early genera. The width and height of the lobes in respect to shell size is much greater than that of the earlier genera. The myophore faces are rotated in the posterior direction, more than 90° from the plane of commissure. The myophores are deep, narrow slots in the posterior edge of the lobes.

*Bellimurina,* and *Oslomena* have cardinal process lobes different from those of *Murinella.* They resemble the knob-like lobes of some species of *Dactylogonia* but they are minute. The lobes of *Limbimurina* are known from one specimen. They are similar to the elongated, cupped lobes of some species of *Dactylogonia* and *Cyphomena.*

The cardinal process lobes of the Leptaeninae are subject to evolutionary modification throughout the long history and the many genera and species of the subfamily.



*Text-figure 20.*—The cardinal process and related structures of the dorsal valve of selected strophomenacean genera.

The earliest species of the Leptaeninae, *Leptaena rugosa* Dalman and *L. ordovicica* Cooper, have parallel, blade-shaped lobes with a wide cleft. The myophore is located on the dorsally inclined, posterior edge of the lobe. If younger species and genera are observed several progressive effects may be noted. The anterior end of the cleft remains wide, but the posterior end of the cleft becomes narrow until in Devonian varieties of *Leptaena rhomboidalis* [?] (Wilckens) and the Mississippian species *Leptagonia analoga* (Phillips) the posterior ends of the lobes are fused together in the manner of some orthotetids. The distal ends of the lobes tend to converge over the cleft in younger species. The result is a broad shallow chamber in place of the anterior end of the cleft. Also, in younger species, there is a tendency for broadly petaloid or cupped myophores to develop. The petaloid myophore may be large and gently inclined on *L. richmondensis* Foerste, *Kiaeromena kjerulfi* (Holtedahl), *Megamyonia unicostata* (Meek and Worthen), and some varieties of *Leptaena rhomboidalis* (Wilckens).

The irregular, knoblike lobes of *Leptaenisca* are exceptional. They may be associated with the cemented habit of the Leptaenoideinae.

The cardinal process lobes of advanced genera of the Oepikinidae and *Rhipidomena* are distinctly different from those of the archaic oepikinids and murinellines. The lobes of *Oepikina, Macrocoelia,* and *Rhipidomena* are short (posterior to anterior), broad (medial to lateral), tall hemicylinders. They stand normal to the plane of commissure and flush with the posterior margin of the valve. These cylinders generally bear deeply folded or cupped myophores on the posterior surface. The cleft is narrow and tends to converge to a thin slit between the posterior bases of the lobes. The myophore surfaces on the posterior faces of the lobes are convergent toward the apex of the dorsal valve. The cardinal process lobes of *Macrocoelia* and *Rhipidomena* differ from the description, which applies to *Oepikina,* only by being slightly more elongated in a posterior to anterior direction than the lobes of *Oepikina*. The right cardinal process lobe of *Oepikina* commonly is distorted. Deformation of a cardinal process lobe is not common in other genera.

The cardinal process of the Rafinesquinidae has a great range of size through the various species. The cardinal process of *Pionomena* is unknown. The only known cardinal process of *Colaptomena* is broken. The one incomplete lobe seems to more closely resemble the lobes of *Oepikina* than any rafinesquinoid species. The lobes of *Kjaerina, Hedstroemina* and older species of *Rafinesquina* are elongated, erect, delicate blades. The blades of *Hedstroemina* are widely separated and nearly parallel. The blades of *Kjaerina* and older species of *Rafinesquina* are widely separated to the anterior. They converge but do not unite toward the posterior. The myophores are situated on the steeply inclined posterior edges of the lobes. These delicate blades resemble the juvenile cardinal process blades of advanced species of *Rafinesquina.* The bases of the cardinal process lobes of advanced species of *Rafinesquina* are elongated and strongly convergent toward the posterior; some bases may be overgrown with secondary shell tissue. The distal terminations of the blades are greatly expanded petaloid or flatiron shaped platforms. The myophore surfaces are inclined so as to face in the posterior-dorsal direction. The posterior bases of the myophores converge toward the apex of the valve under the chilidium. These are the largest cardinal process lobes in the Strophomenacea. There is an interesting parallelism of the bladelike lobes of the older species of leptaenids and rafinesquinids and the petaloid lobes of the younger species of leptaenids and rafinesquinids.

As noted, the earliest strophomenid, *Rhipidomena,* has a cardinal process resembling the advanced oepikinids. From this beginning, the strophomenid groups, Glyptomenini, Furcitellini, and Strophomeninae diverge strongly in the character of the cardinal process. The cardinal process lobes of the advanced Glyptomenini and *Teratelasma* are minute in relation to shell size. They are tiny nodes or hemispheres at the medial-posterior ends of the socket buttresses. The nodes are flush with the posterior margin of the valve. The myophores are shallow excavations in the posterior faces of the nodes. The cardinal process lobes of *Foliomena* either are absent or submerged in secondary shell tissue. Species of the Furcitellini possess cardinal process lobes which bear a strong resemblance to that structure in *Dactylogonia* and *Cyphomena.* This is another example of the striking convergence of this group and the archaic leptaenids.

The cardinal process of the Strophomeninae is reminiscent of this structure in *Oepikina.* The lobes are hemicylindrical and broader than they are long. They bear deeply folded or cupped myophores. The lobes of the Strophomeninae differ from the lobes of the Oepikinidae by being slightly smaller and more delicate relative to shell size, more closely spaced together, and slightly inclined. The myophore face of gerontic specimens of younger species may be petaloid or grossly enlarged and the bases of the lobes may be overgrown with secondary shell tissue.

The general evolutionary trends of the cardinal process lobes of the Strophomenacea seem to be toward increased size, shortening in the posterior-anterior direction, increased area of the myophore and inclination of the myophore. The Glyptomenini and advanced Murinellinae are the principal exceptions to this generality. The changes which accompany the growth of individuals approximately duplicate the phylogenetic trends. The tendency of gerontic individuals to bear elaborately expanded or cupped myophores which are less steeply inclined than those of juveniles is particularly noticeable.

*Socket buttress.* — The shape of the socket buttress, the profile of the valve and the dental angle undergo collateral changes in the evolution of the Strophomenacea. As has been noted, the dental angle is inversely related to the length of the interareas and the size of the pseudodeltidium. The socket buttresses mate with the teeth, consequently the dental angle controls the angle formed by the socket buttresses. As there is a general tendency for the dental angle to increase throughout the phyletic history of the Strophomenacea, the angle formed by the socket buttresses also increases with phyletic advance. This general tendency is partly obscured by the variable amount by which the socket buttress may overhang the cavity of the socket. In those groups with greatly projecting teeth or receding dental lamellae, as the Oepikinidae and the Strophomeninae, the socket buttresses hook further under the teeth then in the groups with pronounced dental lamellae or delicate teeth. For the purpose of description, the angles between the lateral-posterior edges of the socket buttresses may be small (up to 100°), moderate (100 to 120°), or large (greater than 120°).

The archaic oepikinids and leptaenids have long socket buttresses that are set at a moderate to large angle. The buttresses are long because the teeth are long and prominent. The lateral-posterior edge of the socket buttresses may or may not project strongly above the internal surface of the valve. If the profile of the valves is biconvex, the socket buttress is a prominent ridge, but if the profile of the valves is concavo-convex, the socket buttresses are low ridges which may be almost flush with the internal surface of the valve.

The advance leptaenids have short, obscure socket buttresses that are set at a small angle. The socket buttresses are scarcely longer than the length of the ventral interarea. Apparently the posterior end of the socket buttress hooks under the posterior end of the tooth into the space occupied by the fully developed dental lamellae of other groups. In this way, the angle formed by the lateral edges of the socket buttresses is quite small.

The socket buttresses of the advanced oepikinids and the rafinesquinids are set at a moderate angle. Among the advanced oepikinids, the buttresses are short and very prominent. This form is the result of articulation of the buttress with only the thick, blunt anterior projection of the tooth. The rafinesquinids have moderately long, projecting socket buttresses. The length of the buttress results from its mating with the long edge of the tooth along the dorsal margin of the delthyrial chamber. The buttress projects into the delthyrial chamber and consequently is a high ridge.

The socket buttresses of the Strophomenidae, in general, are long, curved, and prominent. They are set at a small to large angle depending upon the length of the ventral interarea, which is variable in this family. The posterior end of the buttress may completely overhang the socket so that the lateral-posterior edge of the buttress directly overlies the lateral socket buttress. The lateral-anterior end of the socket buttresses are reflexed toward the interarea. The reflexed curvature of the buttress in many species is accompanied by elevation of the surface of the fulcral plate plus secondary deposits across the entire floor of the socket. The entire socket and buttress is thus set apart from the rest of the internal surface of the valve.

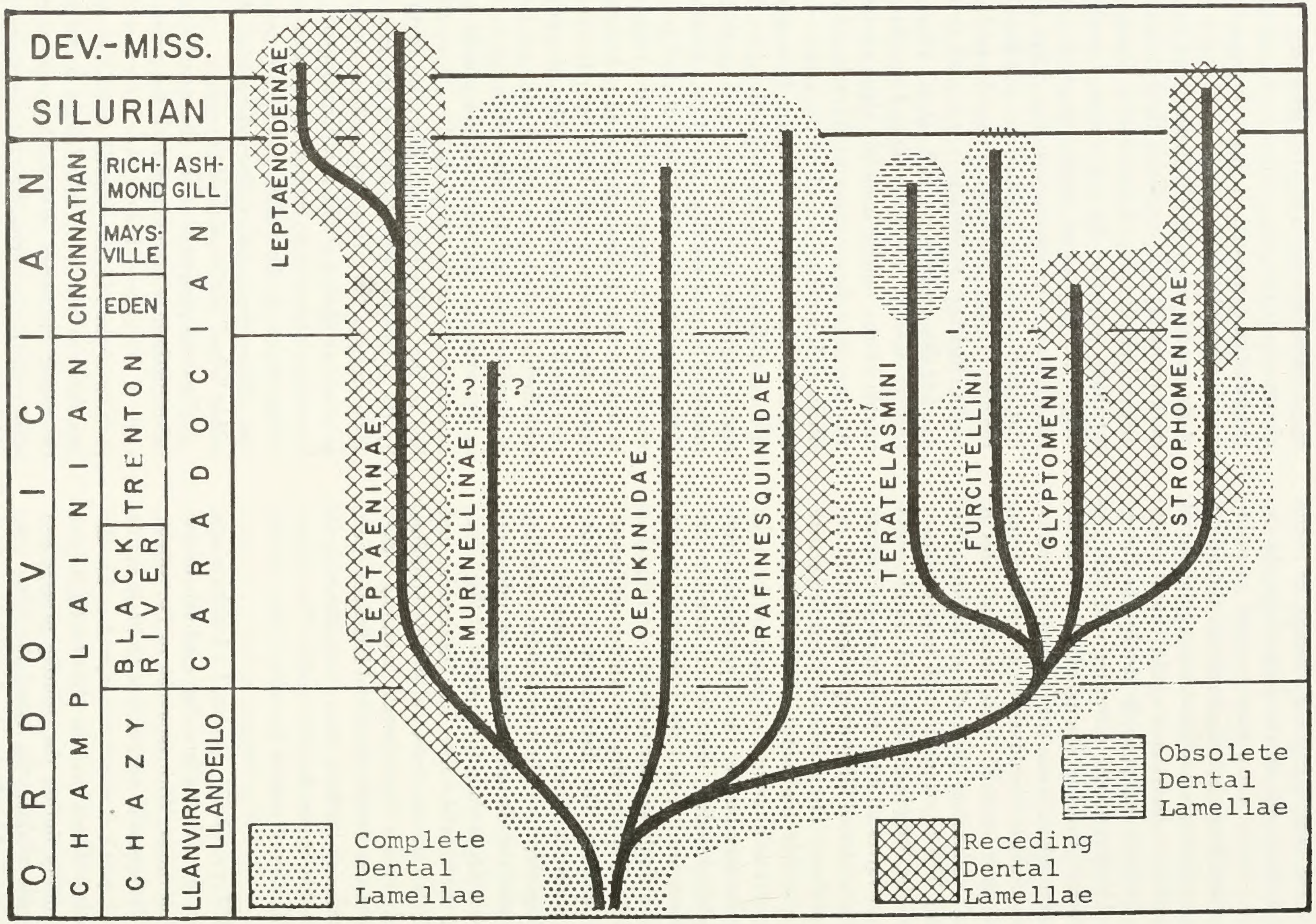
The curvature of the socket buttress and the elevation of the surface of the fulcral plate plus secondary deposits in the socket are characteristic of strophomenoids which have plano-convex, biconvex, and resupinate profiles. These features are not restricted to the Strophomenidae but also occur in biconvex *Murinella* and some of the other leptaenids which tend to have biplanate or biconvex valves posterior to the geniculation. That is, these features are found only in those strophomenaceans in which the dorsal valve tends to be flat or arched away from the plane of commissure. Apparently the curvature of the buttresses and the layer of secondary tissue is required to lift the socket into the plane of commissure.

*Dental lamellae.* — Changes in the form of the dental lamellae are antithetic to changes in the socket buttresses with respect to variation in the profile of the valves. The fulcral point of the tooth-socket articulation must lie on the hinge line of the valves. The plane of commissure, which is defined by the line of contact of the two valves around their periphery, passes through the hinge line. If the arch of the ventral valve is directed toward the plane of commissure, that is, if the ventral valve is concave, or if the ventral valve is flat, the height of the teeth above the internal surface of the ventral valve must be small to maintain the fulcrum on the hinge line. Reduction of the height of the teeth apparently is accomplished in strophomenoid evolution by reduction or obsolescence of the dental lamellae which support the teeth and possibly also by the curvature of the teeth. This hypothesis correlates well with the condition of the dental lamellae throughout the Strophomenacea. The genera which have convex ventral valves, whether the entire profile be biconvex or concavo-convex, generally have completely formed dental lamellae. This is the condition in the Oepikinidae, Murinellinae, Rafinesquinidae, and Furcitellini. The Leptaenidae with largely planate ventral valves and the Strophomeninae and *Rhipidomena* with concave ventral valves all have receding or obsolescent dental lamellae. The advanced Glyptomenini present an exception to this hypothesis. The profile of all of the genera of this tribe is flat, either biplanate, or weakly concavo-convex or resupinate. The interareas of genera in this tribe are narrow. All of the members of the Glyptomenini have fully formed or slightly receding, short dental lamellae. Apparenty if both valves are flat and the interareas are narrow, the fulcrum of articulation has to lie on the hinge line and there is no mechanical necessity for evolutionary recession of the dental lamellae. The distribution of variations upon the dental lamellae is shown in Text-figure 21.

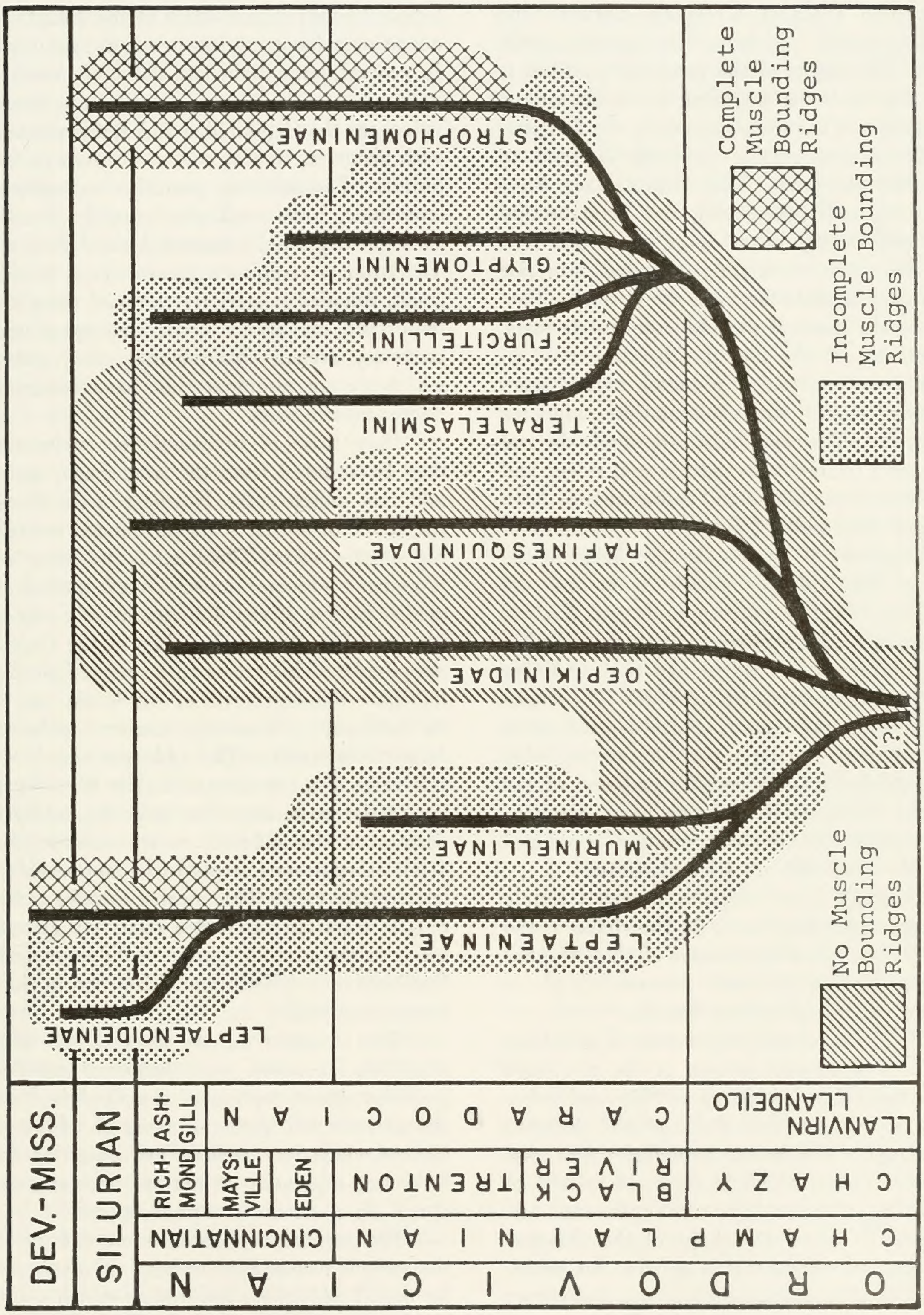
*Muscle bounding ridges.* — The Leptaenidae, excluding some murinellines, and the Strophomenidae, excluding the Teratelasmini, possess ridges along the margins of the diductor muscle scars in the ventral valve. The Oepikinidae and the Rafinesquinidae largely are devoid of muscle bounding ridges. As has been noted, these muscle bounding ridges are histologically continuous with the dental lamellae. There is a physical discontinuity between these structures only in genera which have obsolescent dental lamellae. Text-figure 22 shows the distribution of muscle bounding ridges in the Strophomenacea.

Spjeldnaes (1957, pp. 42-49) presented a lucid account of the mechanics of the diductor muscles, cardinal process and muscle bounding ridges. With reference to Dr. Spjeldnaes' discussion of the muscular system, pp. 42-49, it should be noted that fig. 13, p. 43, does not correspond to his discussion. Dr. Spjeldnaes told me that the plate for fig. 13 was disassembled accidentally during the printing process and reassembled incorrectly without his knowledge. The substance of his discussion is that the mechanical advantage of the diductor muscles is greatest when the vector of pull of the muscles is along the midline of the valves and at 90° to the valve being rotated. If this is the case, the lifting of the muscle scars above the general level of the internal surface of the ventral valve by the muscle bounding ridge and the thick secondary deposits within the muscle field impares the mechanical efficiency of the muscles. This is true, but other attributes imparted by the muscle bounding ridges outweigh the mechanical disadvantage of elevation of the muscle scars. The muscle bounding ridges along the lateral margins found in the Leptaenidae and Furcitellinae confine the muscle attachment sites to near the midline of the valves where efficiency is greatest. It is curious that the Oepikinidae and Rafinesquinidae lack lateral ridges, not that the Leptaenidae and the Furcitellinae have them. The anterior margin of the muscle bounding ridge confines the muscle attachment to the posterior medial region of the valve where efficiency is greatest, *i.e.* where the vector of pull is nearest to 90° to the valve being rotated. Moreover, the measure of a muscle's power is not proportional to the area of the muscle scar but rather to the cross sectional area of the muscle. The anterior elevation of the diductor muscle scars of the Strophomeninae and some of the Leptaenidae by the muscle bounding ridges permitted the muscles to be ovoid in cross section. If these genera had lacked muscle bounding ridges, the muscles would have been flattened sheets with very small cross sectional area. Also, if a strophomenacean with highly arched, resupinate profile, as found in species of *Strophomena,* had flabellate diductor muscles as found in *Rafinesquina,* the portion of the muscle attached in the anterior region of the muscle field could not follow a straight line to the cardinal process. Elevation of the muscle field by the ridges permits all parts of the muscle scars to lie along straight lines from the cardinal process. Hence, the principal attributes of the anterior segments of the muscle bounding ridges were to confine the muscles to the posterior-medial region of the valves, to increase the cross sectional area of the muscle and to place all parts of the muscle field within "view" of the cardinal process.

*Posterior platform.* — The shape and height of the posterior platform is interrelated with the profile of the valves, angle of divergence of the socket buttresses and shape and position of the adductor muscle scars. The posterior-lateral boundaries of the lateral ridges of the posterior platform are the socket buttresses. Hence, those genera which have a small angle of divergence between the socket buttresses, *i.e.* which have long ventral interareas and complete dental



*Text-figure 21.*—The nature of the dental lamellae throughout the Strophomenacea.



*Text-figure 22.* — The condition of the diductor muscle bounding ridges of the Strophomenacea.

lamellae, have a small angle of divergence between the lateral ridges of the posterior platform. The opposite condition holds, as well. The height of the posterior platform is related to profile, just as is the height of the socket ridges. Lineages of resupinate and biconvex genera, *i.e.* the Strophomeninae, Furcitellinae, and archaic murinellines, tend to have high posterior platforms. The Oepikinidae, Rafinesquinidae, Leptaeninae, Glyptomenini, and Teratelasmini which have flattened, weakly biconvex or concavo-convex profiles tend to have low to slightly elevated posterior platforms. The anterior-lateral margin of the posterior platform is controlled by the shape of the adductor muscle scars. The anterior-lateral tip of the lateral ridge is curved in genera with circular or subcircular adductor muscle scars and straight among genera with subquadrate adductor muscle scars. Thus, the older oepikinids, rafinesquinids, and all strophomenids have relatively straight lateral ridges and the leptaenids, advanced oepikinids and rafinesquinids have curved lateral ridges. The width (posterior to anterior) of the lateral ridges is governed by the distance between the posterior margin of the adductor muscle scars and the cardinal process. The primitive rafinesquinids and *Kirkina* have wide lateral ridges, the strongly resupinate strophomenins have very narrow lateral ridges and the remaining genera have lateral ridges of intermediate width. The length of the medial ridge of the posterior platform depends upon the length of the adductor muscle scars. The medial ridge tends to bifurcate at the anterior end for emission of the breviseptum in the Oepikinidae, Murinellinae, Strophomeninae, and Furcitellini. The Glyptomenini have a reduced to absent medial ridge from the posterior platform.

The interplay of all these variables prevents simple description of the changes which occur in the shape of the posterior platform in the evolving lineages of the Strophomenacea. Text-figure 20 illustrates the characteristic shape of the posterior platform of the various lineages.

*Muscle scars.* — The taxonomic importance of the shape of the diductor muscle scars and pattern of the myophore ridges has been stressed by Spjeldnaes (1957) and other authors. Inasmuch as the size and shape of the diductor muscle scars are related to the muscle bounding ridges, discussed in a previous section, which in turn are related to profile, the diductor muscle scars have some taxonomic importance. Text-figure 16 shows the shape of the diductor muscle scars of a few strophomenacean genera. An evolutionary sequence of the diductor muscle scar size and shape, except as related to evolution of profile, cannot be established. The myophore ridges of the diductor muscle scars do not seem to have any taxonomic or evolutionary importance. In general, large, flabellate diductor muscle scars are found in families with concavo-convex, not strongly geniculated valves, as the Oepikinidae and Rafinesquinidae. The groups with biconvex, weakly concavo-convex or weakly resupinate profiles, Furcitellinae, primitive rafinesquinids and most leptaenids, have incomplete muscle bounding ridges and consequently long, subparallel sided diductor muscle scars. The strongly resupinate genera of the Strophomeninae have small, rounded posteriorly confined muscle scars. The only important exceptions occur among genera of the Leptaeninae, archaic Murinellinae and archaic Oepikinidae which are not resupinate but have posteriorly confined diductor muscle scars.

Very little of taxonomic or evolutionary importance may be adduced from the size, shape, and position of the adductor muscle scars. Nowhere in the Strophomenacea are the adductor muscle scars surrounded entirely by the diductor muscle scars. There tends to be a wider and more prominent adductor muscle track leading to the anterior-medial border of the diductor muscle scar in the Leptaenidae and Strophomenidae than in the Oepikinidae or Rafinesquinidae. This seems to be related simply to the larger, flabellate diductor scars of the latter two families relative to the small, posteriorly restricted diductor scars of the former two families. The adductor muscle scars in the ventral valve of a few leptaenids, *e.g. Megamyonia,* may be set far to the posterior, even into the delthyrial cavity. The position of the adductor muscle scars in the ventral valve of all other groups seems to be comparable relative to the apex of the valve. This means, therefore, that the adductor muscle scars are situated a relatively greater distance posterior to the anterior margin of diductor muscle scars in the Oepikinidae and Rafinesquinidae than in the Leptaenidae or Strophomenidae.

The adductor muscle scars of the dorsal valve have negligible taxonomic or evolutionary significance, also. The posterior dorsal septum of the Oepikinidae clearly divides the anterior and posterior pairs of adductor muscle scars. Genera which lack well-defined posterior dorsal septa also lack clear separation of the muscle scar pairs. The anterior dorsal septa are not transmuscle septa.

The archaic oepikinids, some murinellines and all of the strophomenids tend to have subquadrate to subtriangular dorsal adductor muscle scars which commonly are split by the posterior dorsal septa. The posterior margin of these muscle scars seems generally to be straight and perpendicular to the medial ridge of the posterior platform. In the Leptaenidae and Rafinesquinidae, and to a lesser extent in the advanced Oepikinidae, there is a strong tendency for the adductor muscle scars to be subcircular.

*Size.* — The mean size of species does not seem to have any great taxonomic or evolutionary significance above the generic level in the Strophomenacea. There does seem to be a vague tendency in the Strophomenacea for increase of size throughout the history of the superfamily. For example, species of *Rafinesquina* and *Strophomena* of Cincinnatian age generally are larger than species of these genera of Trenton age; most species of *Oepikina* are larger than species of *Dactylogonia* or *Hesperinia; Leptaena rhomboidalis* Wilckens from the Devonian is larger than *L. richmondensis* Foerste or *L. ordovicica* Cooper from the Ordovician. Species of the Strophomenacea are so numerous and exceptions to this trend are so common that statistical confirmation would be most difficult to establish. Moreover, exceptions to the tendency for increased size are so numerous that size could not be useful either as an indicator of geological time or evolutionary position of a species within the superfamily.

The mean size of adult individuals is a useful feature for diagnoses of species but not for genera or families. Many genera include species of greatly differing size. For example, an adult specimen of *Rafinesquina mucronata* Foerste measures 19 mm wide whereas an adult specimen of *R. loxorhytis* (Meek) measures 76 mm wide, a gerontic specimen of *Strophomena parvula* Foerste is 14 mm wide whereas an adult specimen of *S. vetusta* (James) is 46 mm wide. Reference to size in generic or familial descriptions applies only to known species and should not bias the allocation of future discoveries.

*Prosopon.* — The distribution of patterns of prosopon in the strophomenacea does not seem to follow any evolutionary progression. Moreover, the patterns of prosopon show little restriction to suprageneric taxa. All attempts to base phylogeny upon pattern of prosopon have led to aggregations of species that are incompatible in internal characteristics. This is a curious situation because the fine costation, but not rugae, would seem to have the least adaptive valve of all strophomenacean features. At best, some genera may be distinguished by prosopon, for example, the cymostrophioid pattern which distinguishes *Gunnarella* and the ptychoglyptoid pattern which marks *Bellimurina.* Other genera may incorporate species with dissimilar prosopon patterns, for example, the rafinesquinoid pattern of *Oepikina speciosa* Cooper and the strophomenoid pattern of *O. gregaria* Cooper.

If the many exceptions are ignored, the various families do show ill-defined differentiation by radial prosopon patterns. The earlier oepikinids are coarsely and uniformly costate (*Hesperinia*), glyptomenoid (*Dactylogonia*), or rafinesquinoid (*Kirkina*). Other oepikinids are either rafinesquinoid or strophomenoid. The murinellines are nervose (*Murinella*), coarsely and uniformly costate (*Murinella* and *Cyphomena*), or ptychoglyptoid. The Leptaeninae is all coarsely and regularly costate with a few exceptional occurrences of the rafinesquinoid pattern. The Rafinesquinidae are all rafinesquinoid. The Glyptomenini are glyptomenoid. The Furcitellinae and *Teratelasma* are uniformly costate. *Foliomena* is smooth. The Strophomeninae includes species which are strophomenoid, rafinesquinoid, or scoticoid.

The poor correlation of prosopon patterns and families is disturbing. Possibly the prosopon patterns have not been correctly defined or possibly the prosopon patterns have not been differentiated in sufficient detail.

The occurrence of rugae is not taxonomically restricted. Most genera of the Leptaeninae are rugose but rugation also occurs in species of *Oepikina, Rafinesquina, Kjaerina, Actinomena, Luhaia,* and *Strophomena.* Concentric rugation seems to be correlated with strongly oblate or subrectangular shape and geniculation. Possibly these characters are somewhat interdependent. Oblique rugae, however, seem to occur on resupinate or concavo-convex species which are prolate and highly arched but not geniculate.

A kjaerinoid costa is found most commonly on early species and juvenile individuals of the Rafinesquinidae. In addition, a kjaerinoid costa occurs on some species of *Kjerulfina* and *Megamyonia.* Both of these genera have some rafinesquinid characteristics. Because the costa does not occur on all species of these genera, its presence is considered to be homeomorphic and not indicative of relationship.

*Meso-cardinal ridge.* — The meso-cardinal ridge is a gerontic feature of strophomenaceans (Text-figure 28). Consequently, the occurrence of this feature is not consistent among the individuals of a species. It is common to find that all of the individuals in a collection of a species will possess a meso-cardinal ridge. The larger size, thicker shells, and more prominent features of gerontic individuals cause them to be more resistant to fracture and more attractive to collectors. Not all specimens of young individuals of the same species will show the meso-cardinal ridge. The meso-cardinal ridge is a more prominent feature of the Leptaenidae, Oepikinidae, and Rafinesquinidae than of the Strophomenidae. This structure in the Strophomenidae is located on the medial-posterior base of the cardinal process under the chilidium. It may be observed in this family only in sections or in exceptionally preserved specimens.

*Vasculae.* — The vascular channels of the Strophomenacea rarely are well preserved. Specimens commonly possess ill-defined vascular markings which are too faint to permit analysis of the complete pattern. The few relatively complete patterns which have been observed seem to be saccate, inequidistributate in both valves. The lemniscate pattern figured by Williams (1956, p. 274) for the ventral valve of *Strophomena* cannot be supported. If the vascular pattern of *Foliomena* is digitate, as tentatively proposed by Williams (1965, p. H391), the genus is unique in the superfamily in respect to vasculae.

European specimens more commonly show well-preserved vascular markings than specimens from North America. It is tempting when first noticed to attribute this situation to special taxonomic lineages or special environmental conditions as water temperature or quantity of available oxygen. Such is not the explanation. The European specimens commonly are preserved in the form of molds and illustrated as such. A natural mold characteristically shows a more complete vascular pattern than the complementary shell. The internal surfaces of dried specimens of terebratuloids generally show the vascular patterns as granular, brown crusts, possibly of coagulated coelomic fluid. If these crusts are brushed or scraped away, there are no vascular channels evident in the shell. Apparently, the vascular sinuses influenced the deposition of sediment adjacent to the internal surfaces of the valves of a strophomenacean shortly after its death.

## HISTOLOGY

*Composition.* — The shell material of unaltered fossil articulate brachiopods is composed largely of calcium carbonate in the form of calcite. Quantitative chemical analyses and optical mineralogical analysis of articulate brachiopod shell have been presented by Clarke and Wheeler (1915, 1917) and Hobbs and Cloud (1942). Clarke and Wheeler reported that modern articulate brachiopods contain from 52% to 55% CaO, 44% to 45% organic combustibles and less than 0.5% each of $SiO_2$, $(AlFe)_2O_3$, MgO, $SO_3$ and $P_2O_5$. Recalculation of oxide percentages to carbonate percentages with omission of the organic combustibles, by Clarke and Wheeler, reveals that the inorganic fraction of modern articuate brachiopod shells is 97% to 99% $CaCO_3$.

There are no published chemical or optical analyses of strophomenoid brachiopod shells. Mr. John Shade, Miami University, Department of Geology, performed x-ray fluorescence analysis of *Strophomena planumbona* (Hall). Analysis was made with a chromium tube and sodium chloride analyzer crystal. Unweathered specimens of single valves of exceptional initial cleanliness were selected for analysis. The surfaces were scraped with a steel blade to remove all clay and silt particles. No preparatory reagent other than hydrogen peroxide was used to loosen clay and silt. The $K\alpha$ and $K\beta$ maxima of calcium were the only strong maxima of the spectrogram. Other maxima not attributable to the tube and columnator include the $K\alpha_1$, $K\alpha_2$ and $K\beta_1$ maxima of iron, the $K\alpha$ maximum of strontium, questionably the $K\beta$ maximum of rubidium and an unidentified maximum at about 6.8° $2\theta$. There are no maxima to indicate the presence of silicon, phosphorus, or aluminum. Magnesium and sulphur are too light to be detected conveniently by this technique.

Samples of crushed strophomenacean brachiopod shells have been examined with a petrographic microscope. The individual crystalline bodies of which the lamina of the shell are composed are too small to be resolved clearly and, consequently, are too small for positive optical identification. Hobbs and Cloud concluded that the shell material is calcite because its refractive index is within the calcite range which is less than the refractive index range of aragonite. They noted, also, that cleavages of the crystalline bodies were oriented as would be expected in calcite and not as in fibrous aragonite. Hobbs and Cloud could not present conclusive optical identification because the grains they observed gave biaxial interference figures, although calcite is uniaxial. They postulated that the biaxial character of the calcite originated from strains generated in the process of grinding sections. Sass, Monroe, and Gerace (1965) illustrated the crystalline bodies by electron photomicrographs of sections of the shell of *Pictothyris picta* (Dillwyn) and *Gryphus stearnsi* (Dall and Pilsbry). Sass, *et al* stated that the crystalline bodies are calcite but do not support their identification.

X-ray diffractograms of crushed shells of *Rafinesquina ponderosa* Ulrich and *Strophomena planumbona* (Hall) have been made by Dr. Taki Negas, The Ohio State University, Department of Mineralogy. Specimens were prepared for analysis as described above. Both diffractograms show

Table 2. — Nomenlature of the shell layers of articulate brachiopods.

| AUTHOR | ← EXTERNAL SURFACE OF VALVE | | INTERNAL SURFACE OF VALVE → | |
|---|---|---|---|---|
| Shrock and Twenhofel (1953) | Periostracum | Outer carbonate layer<br>Lamellar or Lamellate layer<br>middle layer<br>nonfibrous layer | Inner carbonate layer<br>Prismatic layer<br>fibrous layer | secondary deposits |
| Schuchert and Cooper (1932) | Periostracum<br>Epidermis | outer, first, primary, nonfibrous, lamellar | fibrous | extra shell matter |
| Miloradovitsch (1937), fide, Ager and Riggs (1964) | | | Fibrous layer | |
| Hobbs and Cloud (1942) | Periostracum | Outer carbonate layer | Inner carbonate layer | |
| Salmon (1942) | | | intermediate layers | |
| Alexander (1948) | | Outer shell layer | Prismatic layer | Inner shell layer |
| Williams (1953) | Periostracum | Outer layer | Internal layer | |
| | | Lamellar layer<br>nonfibrous layer | Inner fibrous layer | Impunctate fibrous material (of muscle attachment sites) Cryptocrystalline material (of tendenous patches). |
| Williams (1956) | Periostracum | Primary layer | Secondary layer, in part, Prismatic layer | |
| Vandercammen (1956-1959) fide, Ager and Riggs (1964) | | Fibrotest | Prismotest | Callotest |
| Spjeldnaes (1957) | | Primary layer, external layer | Secondary layer, inner layer | |
| Muir-Wood and Cooper (1960), Muir-Wood (1962) | | Lamellar layer | Fibrous layer | granular material |

Capitalization indicates author(s) used name in formal sense; other names used by author(s) in descriptive sense.

that the only important compound in the samples is calcite. A trace of quartz is recorded in both diffractograms. No other mineral constituents are present. Compositional variation cannot be used to explain the color differentiation of the characteristically dark *Leptaena-Rafinesquina* group and the light *Holtedahlina-Strophomena* group.

*Nomenclature of articulate brachiopod shell layers.* — General descriptions of the microscopic structure of brachiopod shells appear in many texts, *e.g.* Shrock and Twenhofel (1953). Descriptions of microscopic structure of the strophomenacean shell were published by Kozłowski (1929), Öpik (1930), Williams (1953a, 1956), and Spjeldnaes (1957). All accounts of brachiopod microstructure convey confusion by (1) the lack of uniformity of nomenclature used to designate the four layers of the brachiopod shell, (2) oversimplification of the character and homogeneity of each of the four layers and (3) oversimplification of the differentiation of the shell layers. Variance in the nomenclature of shell layers is summarized in Table 2.

Inspection of Table 2 demonstrates the general lack of agreement for shell-layer nomenclature. Disagreement stems from variations in shell structure of different brachiopod groups studied by authors and from different methods of preparation of specimens for observation. Each of the three shell layers formed by the edge of the articulate brachiopod mantle and the "secondary deposits" formed posterior to the mantle edge are assumed to be homologous throughout the class. This assumption is made on the basis of gross microstructural similarity, relative thickness, compositional uniformity, and disposition in important macroscopic structures of each of the layers in representatives of different suborders. Lack of homology of the four shell layers of extinct suborders of articulate brachiopods would be difficult to establish because the character of secretory cells and mantle-edge grooves and lobes cannot be studied. Consequently, it is considered prudent to adopt a shell layer nomenclature related to the position of the layer within the entire shell, not to microstructure.

The nomenclature of Hobbs and Cloud (1942), Shrock and Twenhofel (1953), Williams (1953a, 1956), and Spjeldnaes (1957) are nonstructural. Shrock and Twenhofel's system is inappropriate because the "secondary deposits" are carbonate and lie on the inner surface of the "inner carbonate layer". Williams' and Spjeldnaes' classifications are not suitable because the inner-most deposits (Shrock and Twenhofel's "secondary deposits") are formed later than the adjacent "secondary layer" and because the "periostracum", "primary layer", and "secondary layer" are all primary in that they are initiated at the growing margin of the mantle. The words "primary" and "secondary", in this context, should be discarded from shell-layer terminology because of ambiguity.

An emended system of shell-layer nomenclature is illustrated in Text-figure 23. The inner initial layer is initiated at the mantle margin but may be thickened by continued deposition posterior to the margin. The boundary between the initial layers and the secondary deposits consequently is indistinct. The general names of the shell layers in the emended system may be applied to all articulate brachiopods. Names based upon microstructural characteristics may be substituted for the general names in descriptions of specific brachiopod groups. The emended shell-layer nomenclature is employed in the sections which follow.

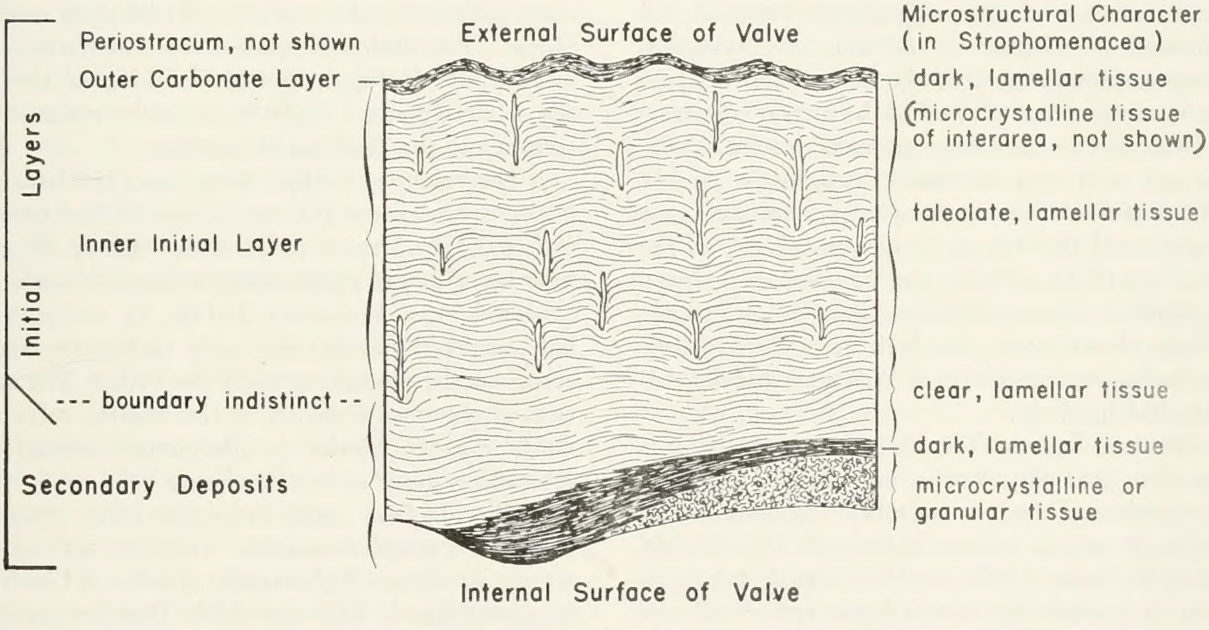
In cases where only part of a layer is being described, the shell material will be called "tissue", as inner initial tissue and outer carbonate tissue. Zoologists have disapproved of this usage of "tissue". However, this paleontological usage is defensible on the following grounds: (1) Structural parts of a shell are called tissue by convention. (2) Shells, although not made entirely of living cells, have the function of an organ in that they provide an animal with a specific service. The structural units of a fleshy organ are tissues; the structural units of a shell should be called tissues also. (3) Shells are products of a distinct organ, in brachiopods, the mantle. Shell tissues are the product of separate mantle tissues.

*Microstructure of the strophomenacean shell.* — The observations to follow were made from study of sagittal, transverse, and longitudinal thin sections and peel sections of strophomenoid brachiopods. Transverse peel sections were most informative, hence were made in greatest number. The species which were studied, the number of specimens sectioned and the number of sections are shown in Table 3.

*Periostracum.* — The periostracum is a thin layer of organic material which covers the external surface of modern brachiopod shells. Williams (1956, p. 249) observed that the periostracum "has never been found in fossils" (brachiopods). No definite periostracum was observed in thin sections or peel sections of Ordovician strophomenaceans. The surface of specimens is rarely covered with a carbonaceous film which might be attributed to the periostracum, as occurs upon molds of associated pelecypods. Black material in grooves in the interareas of *Rafinesquina* may be a carbonaceous residue of periostracum. Thin sections of articu-

Table 3. — Species Sectioned

| No. of Specimens | Species | Sections Thin | Sections Peel |
|---|---|---|---|
| 3 | *Dactylogonia alternata* Cooper. Lenoire Lst.; Friendsville, Tennessee |  | 44 |
| 3 | *Oepikina minnesotensis* (Winchell). Edinburgh Fm.; Rye Cove, Virginia. |  | 66 |
| 3 | *O. gregaria* Cooper. Bromide Fm.; Fittstown, Oklahoma. |  | 68 |
| 6 | *Leptaena richmondensis* Foerste. Liberty Fm.; Camden, Ohio. | 5 | 103 |
| 1 | *L. precursor* Foerste. Arnheim Fm.; Cox Creek, Bardstown, Kentucky. |  | 24 |
| 4 | *Megamyonia unicostata* (Meek and Worthen). Elkhorn Fm.; Hamburg, Indiana. |  | 96 |
| 10 | *Rafinesquina ponderosa* Ulrich. Blanchester Mem., Waynesville Fm.; Bull Run, Oxford, Ohio. | 7 | 205 |
| 10 | *Holtedahlina sulcata* (Verneuil). Whitewater Fm.; Blanchester, Ohio. | 6 | 116 |
| 13 | *Strophomena planumbona* (Hall). Base of Liberty Fm.; Tallawanda Creek at crossing of Butler and Preble Cos. boundary, Ohio. | 4 | 116 |
| 3 | *S. nutans* Meek. Base of Liberty Fm.; west end of Collins Run, Oxford, Ohio. |  | 32 |
| 4 | *S. vetusta* (James). Liberty Fm.; Devil's Backbone, Camden, Ohio. |  | 58 |
| 3 | *S. planoconvexa* (Hall). Fairmount Fm.; Muddy Creek, Cheviot, Hamilton Co., Ohio. |  | 59 |
| 2 | *S. concordensis* Foerste. Arnheim Fm.; Hill's Fork, Adams Co., Ohio. |  | 60 |
| 2 | *Tetraphalerella neglecta* (James). Blanchester Mem., Waynesville Fm.; Collins Run, Oxford, Ohio. |  | 56 |
| 5 | *Thaerodonta rugosa* (Meek). Liberty Fm.; Rt. 127, 2 miles south of Camden, Ohio. |  | 60 |
| 1 | *Fardenia subplana* (Conrad). Waldron Shale; Hartsville, Indiana. |  | 13 |
| 1 | *Schuchertella sp.* Arkona Shale; Arkona, Ontario, Canada. |  | 27 |
| 1 | *Derbyia* cf. *hooserensis* Dunbar and Condra. Camp Creek Shale; Pueblo, McCullock Co., Texas. |  | 33 |
| 5 | *Stropheodonta extenuata* Imbrie. Alpena Lst.; 2 miles west of Alpena, Michigan. |  | 79 |
| 1 | *S. demissa* (Conrad). Silica Shale; Sylvania, Ohio. |  | 20 |
| 1 | *S. heteromys* Imbrie. Bell Shale; Rogers City, Michigan. |  | 17 |


Initial Layers
Periostracum, not shown
Outer Carbonate Layer
Inner Initial Layer
--- boundary indistinct --
Secondary Deposits
External Surface of Valve
Internal Surface of Valve
Microstructural Character
(in Strophomenacea)
dark, lamellar tissue
(microcrystalline tissue of interarea, not shown)
taleolate, lamellar tissue
clear, lamellar tissue
dark, lamellar tissue
microcrystalline or granular tissue

*Text-figure 23.*—A revised nomenclature for the shell layers of strophomenacean brachiopods.

lated specimens, *i.e.* specimens with minimal time between death and burial, with thin bryozoan and coral incrustations were expected to show indication of periostracum between the outer carbonate layer and the incrustation. Either periostracum was absent from Ordovician strophomenaceans, exceedingly thin, or composed of an unstable organic compound not analogous to conchiolin or chitin.

Williams (1956, p. 249) and Spjeldnaes (1957, p. 14) suggested independently the presence of a periostracal "pad" or "ligament" which bridged the hinge line along the interareas of strophomenoids. Their suggestions were based upon the presence of grooves in the interareas which are parallel to the hinge line and upon the convergent attitude of lamellae in the pseudodeltidium and chilidium of strophomenoids. These features may be seen without question, and, as noted, the grooves may be filled with black, carbonaceous-appearing material. Williams (1956, p. 257) reported that the modern thecideoid *Lacazella* possesses a periostracal pad along the hinge line. Spjeldnaes (1957, p. 14) claimed to have observed "a brownish-yellow substance in the frontal [?] part of the pseudodeltidium and chilidium" which he interpreted as remains of a ligament. The outer carbonate layer of the interarea is thick, finely microcrystalline and invariably present in contrast to the thin, discontinuous, lamellar, outer carbonate layer of the rest of the external surface. The "outer carbonate layer" of the interarea is comparable in structure to the finely granular secondary deposits associated with sites of muscle attachment on the internal surfaces of the valves. In the process of making thin sections, it was noted that the microcrystalline tissue of the interareas was less likely to flake than lamellar shell tissue. The microcrystalline tissue possibly possesses greater tensile strength. These observations plus lack of conflicting evidence direct tentative acceptance of Williams' and Spjeldnaes' hypothetical ligament.

*Outer carbonate layer.* — The outer carbonate layer is evident as a thin, granular, fibrous, or lamellar, relatively dark layer in sections of modern articulate brachiopods and representatives of some extinct suborders (spiriferoids, pentameroids). Williams (1956, p. 250) stated, "the primary layer in its typical form is also found sporadically on the shell surface of orthoids and strophomenoids." The present study confirms this observation; the presence of the outer carbonate layer on the disc of the valves is a rare occurrence.

Sections through articulated specimens with bryozoan incrustations reveal the outer carbonate layer under the bryozoan. Outer carbonate layer is not found under all incrustations. Areas of shell surface not protected by bryozoa rarely show the layer. Patches of outer carbonate layer seem to occur most commonly toward the margin of the concave valve; that it, the dorsal valve of *Rafinesquina,* the ventral valve of *Strophomena* and *Tetraphalerella.* The protegulum of *Strophomena planumbona* (Hall), and probably of other species, is composed of outer carbonate tissue.

The outer carbonate layer is difficult to discriminate from the inner initial layer; there is no sharply defined boundary separating the two. Both layers are lamellar in strophomenaceans. The outer carbonate layer tends to be relatively darker than the inner initial layer as observed in peel sections because the lamellae of the outer carbonate layer are consistently thinner than the lamellae of the inner initial layer and the lines separating the lamellae thicker and darker than those of the inner initial layer. The outer carbonate layer is not penetrated by taleolae. Lamellae of the outer carbonate layer tend to be concentric to the costellae of the valve surface and hence are undulatory. Near the margin of the valve, adjacent to the marginal diaphragm and outward to the edge of the valve, the lamellae of the outer carbonate layer and inner initial layer tend to be turbulent. Turbulence is caused by interference from the *vascula terminalia,* marginal thickening of the valve, and the relatively small angle between the plane of transverse section and the direction of costellae.

The valves of *Derbyia hooserensis* Dunbar and Condra, *Fardenia subplana* (Conrad), and *Schuchertella sp.* (all orthotetaceans) seem to be made entirely of outer carbonate layer in the region anterior to the muscle scar areas. *Stropheodonta heteromys* Imbrie (a stropheodontacean) has scattered patches of outer carbonate layer between costae in the central region of the valves. The entire thickness of the central region of the ventral valve of *Thaerodonta rugosa* (Meek) (a plectambonitacean) is coarsely crystalline, outer carbonate tissue.

The thickest outer carbonate layer observed on an Ordovician strophomenacean occurs on the central area of a ventral valve of *Rafinesquina ponderosa* Ulrich. The layer is approximately 0.09 mm thick. Undulations of the layer prevent more precise measurement. The layer is slightly thinner in *Leptaena richmondensis* Foerste and *Megamyonia unicostata* (Meek and Worthen). The thinnest observed section of outer carbonate layer, about 0.04 mm thick, occurs in a specimen of *Strophomena planumbona* (Hall). The extra thickness, persistence, and optical density of the outer carbonate layer of rafinesquinids and leptaenids may account partly for the characteristically darker color of specimens belonging to these families than specimens of oepikinids and strophomenids.

Silica preferentially replaces the inner initial layer and leaves unaltered the outer carbonate layer of *Oepikina gregaria* Cooper. The crests of costellae of *Holtedahlina sulcata* (Verneuil) seem to be outer carbonate layer as the crests lack pseudopuncta. Other species of strophomenaceans show patches of outer carbonate layer in the rugae and major varices around the margin of the valves, especially the concave valve. It is curious that even a clean, well-preserved strophomenoid with finely sculptured, sharp surface detail, does not present an original surface.

A low chamber or tunnel, called here the marginal chamber, leads around the lateral and anterior periphery of the valves. This marginal chamber is formed between the marginal diaphragm and the edge of the valves. The internal surface of valves of *Strophomena* at the site of the marginal chamber is composed of material resembling the outer carbonate layer. A section of one specimen of *Strophomena planumbona* (Hall) which had an unabraded shell edge suggests that this internal peripheral coating is a continuation of the outer carbonate layer from the external surface of the valve. If this is true, it means that the mantle of *Strophomena* was retractile and that dark laminae in the inner initial layer are outer carbonate layer.

Williams (1953a, p. 3) stated that the outer carbonate layer is found upon stropheodontid interareas and is the material of which the pseudodeltidium and chilidium are composed. His observation applies equally to Ordovician strophomenaceans.

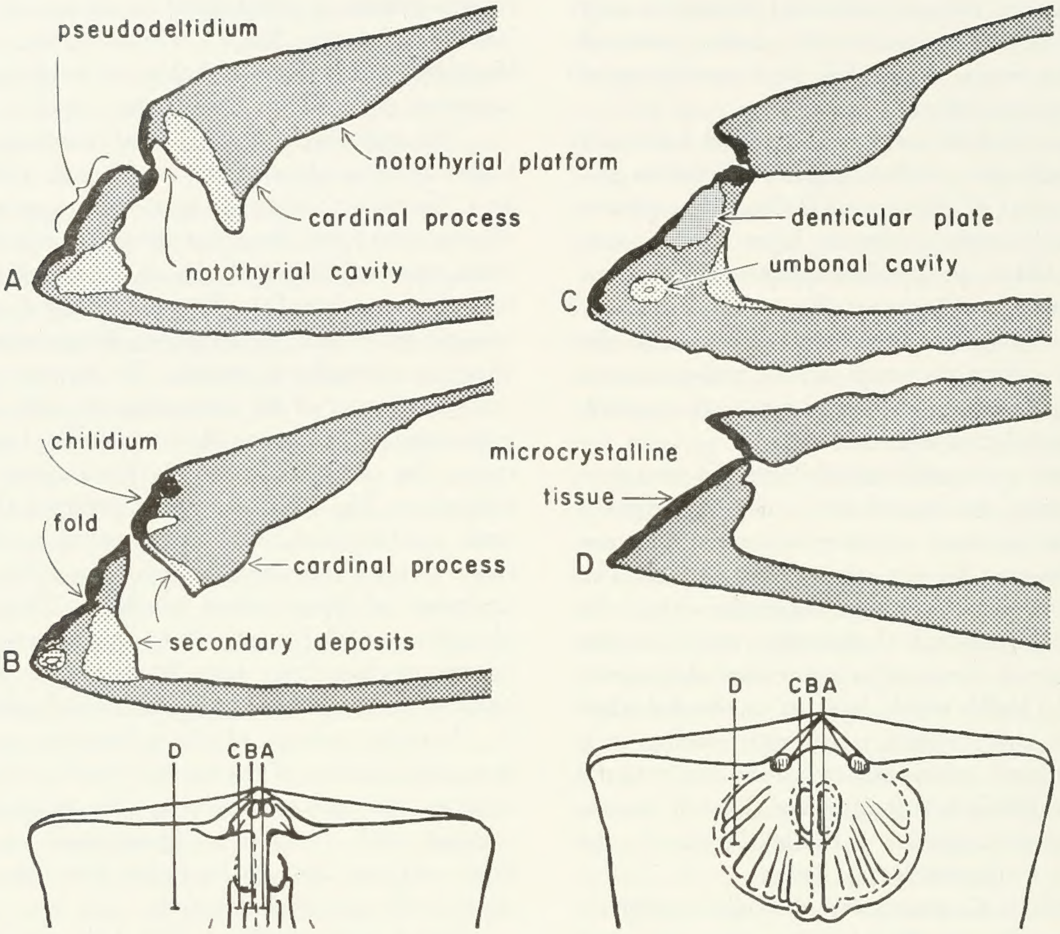
The surface layer of strophomenacean palintropes, the pseudodeltidium, and the chilidium, corresponds to outer carbonate layer in position only. The "outer carbonate layer" of these structures overlies inner initial tissue and is not penetrated by taleolae. The "outer carbonate layer" of the palintrope is thick in comparison to the layer observed on the disc of the valves. The layer is microcrystalline, not finely lamellar. These latter characteristics and lack of evidence of continuity between the outer carbonate layer of the disc and the palintrope suggest that the "outer carbonate layer" of the two regions may not be homologous. Sections of some specimens of *Strophomena* reveal a finely lamellar, nontaleolate layer under the microcrystalline "outer carbonate layer" of the palintrope. This finely lamellar layer is sharply differentiated from the microcrystalline layer but merges without a well-defined boundary into the underlying inner initial tissue. From a microstructural standpoint, this finely lamellar layer is probably the homologue of the outer carbonate layer of the disc of the valves.

The microcrystalline "outer carbonate layer" of the palintrope extends over the length and width of the interarea. Sections parallel to the medial sagittal section (plane of symmetry) but lateral to the teeth and sockets show the cross sectional shape of the microcrystalline layer (Text-figure 24, section D). The microcrystalline layer of the ventral palintrope of *Leptaena richmondensis* Foerste is obtusely triangular in section. The hypotenuse is the interarea; the longer of the two adjacent sides is sutured in an intertonguing fashion to the inner initial layer of the palintrope; the shortest side forms the internal margin of the palintrope. The microcrystalline layer of the dorsal palintrope is a flattened sheet in sectional shape. Microcrystalline tissue forms a parallel-sided layer upon the surface of both interareas of *Rafinesquina ponderosa* Ulrich, *Strophomena planumbona* (Hall), and *Strophomena nutans* Meek. The microcrystalline layer may be joined to the inner initial tissue of the palintrope by a convoluted suture.

External grooves of the palintrope appear as notches in sagittal sections of the microcrystalline layer. Faint variations in the optical density of the microcrystalline tissue correlate with the grooves. These bands are too poorly defined and too faint to be called lamellae. The bands are visible only in sagittal sections.

The microcrystalline tissue of the pseudodeltidium and chilidium is more coarsely crystalline than the microcrystalline tissue of the palintrope. The microcrystalline tissue of the pseudodeltidium and chilidium is obscurely lamellar in sagittal section; the lamellae are thicker and less distinct than lamellae of the inner initial layer. The lamellae correspond to the imbricated rugae on the surface of the pseudodeltidium and chilidium. The medial sagittal groove of the external surface of the pseudodeltidium and chilidium has no microstructural expression. There is no evidence to indicate that the pseudodeltidium originates phylogenetically or ontogenetically from a pair of deltidial plates. The microcrystalline tissue of the pseudodeltidium and chilidium overlies inner initial tissue of the apex of the valves and secondary deposits of the delthyrial and notothyrial cavities.

The pseudodeltidium is irregular to slightly triangular in sagittal section, Text-figure 24, sections A and B. The boundary between microcrystalline tissue of the pseudodeltidium and inner initial tissue is difficult to detect but



*Text-figure 24.*— Parallel sagittal sections through the posterior region of *Strophomena planumbona* (Hall). Outline drawings below, dorsal valve left and ventral valve right, show the course of the sections. Section A does not pass through the apex of the valves but includes the medial side of a cardinal process lobe. The margin of the chilidium of Section B rests against the posterior edge of a cardinal process lobe, leaving a pocket, the notothyrial cavity (open area). The base of the chilidium of Section B is bulbous and convoluted. A small piece of the denticular plate occurs above the umbonal cavity of Section B. The "fold" in Section B marks the posterior margin of the pseudodeltidium. Specimen from Liberty Formation, Camden, Ohio. Magnification of sections, × 9.5.

appears to be an irregular, intertonguing suture. The center of the dorsal margin of the pseudodeltidium of *Strophomena planumbona* (Hall), Text-figure 24, section A, and some other species, *e.g. S. auburnensis* Fenton, bears a dorsally concave plate which is directed anteriorly into the delthyrial cavity. This concave plate appears to be a receptacle into which was fit the ventral margin of the chilidium when the valves were opened. This concave plate has the same microstructure as the microcrystalline tissue of the pseudodeltidium.

The chilidium resembles the pseudodeltidium in microstructure. Chilidia have the form of thin, flattened sheets obscurely sutured into the inner initial tissue of the dorsal apex. The dorsal surface of the chilidium is not supported by inner initial tissue in central sagittal sections. The cavity beneath the central region of the chilidium is the notothyrial cavity. Inner initial tissue forms a backing to the microcrystalline tissue of the chilidia in lateral sagittal sections. Also, the chilidium may rest upon secondary deposits of the posterior surfaces of the cardinal process lobes. The base of the chilidium tends to be bulbous and convoluted, that is, thicker than the unsupported ventral edge. This indicates that the chilidium became thinner as growth proceeded.

The microcrystalline tissue of the pseudodeltidium and chilidium is a continuation of the microcrystalline, "outer carbonate layer" of the palintrope. This may be demonstrated only in transverse or longitudinal sections of perfectly preserved specimens.

The microcrystalline "outer carbonate layer" of the palintrope along the lateral margins of the pseudodeltidium is exceedingly thin. At this position, the microcrystalline layer passes over the denticular plate of the teeth. The conical or cuneate denticular plate is ankylosed to the medial, dorsal margin of the dental lamella. The dorsal surface of the denticular plate tends to be arched slightly. Consequently, the microcrystalline tissue overlying the denticular plate is slightly arched or reduced in thickness. At this position, the microcrystalline tissue is commonly missing, *e.g.* on *Strophomena planumbona* (Hall), and permits the ridged denticular plate to be seen as a part of the surface of the interarea. As a consequence, not all transverse sections show continuity of the pseudodeltidium and the microcrystalline layer of the palintrope.

The form of the microcrystalline layer of the palintrope in the region marginal to the pseudodeltidium is complex, as shown in Text-figure 25. Evidence of the morphology about to be described has been found in all of the Ordovician strophomenaceans that have been sectioned. Tissue differentiation is sufficiently obscure that the following description of the morphology of the microcrystalline layer cannot be followed in any single set of transverse serial sections.

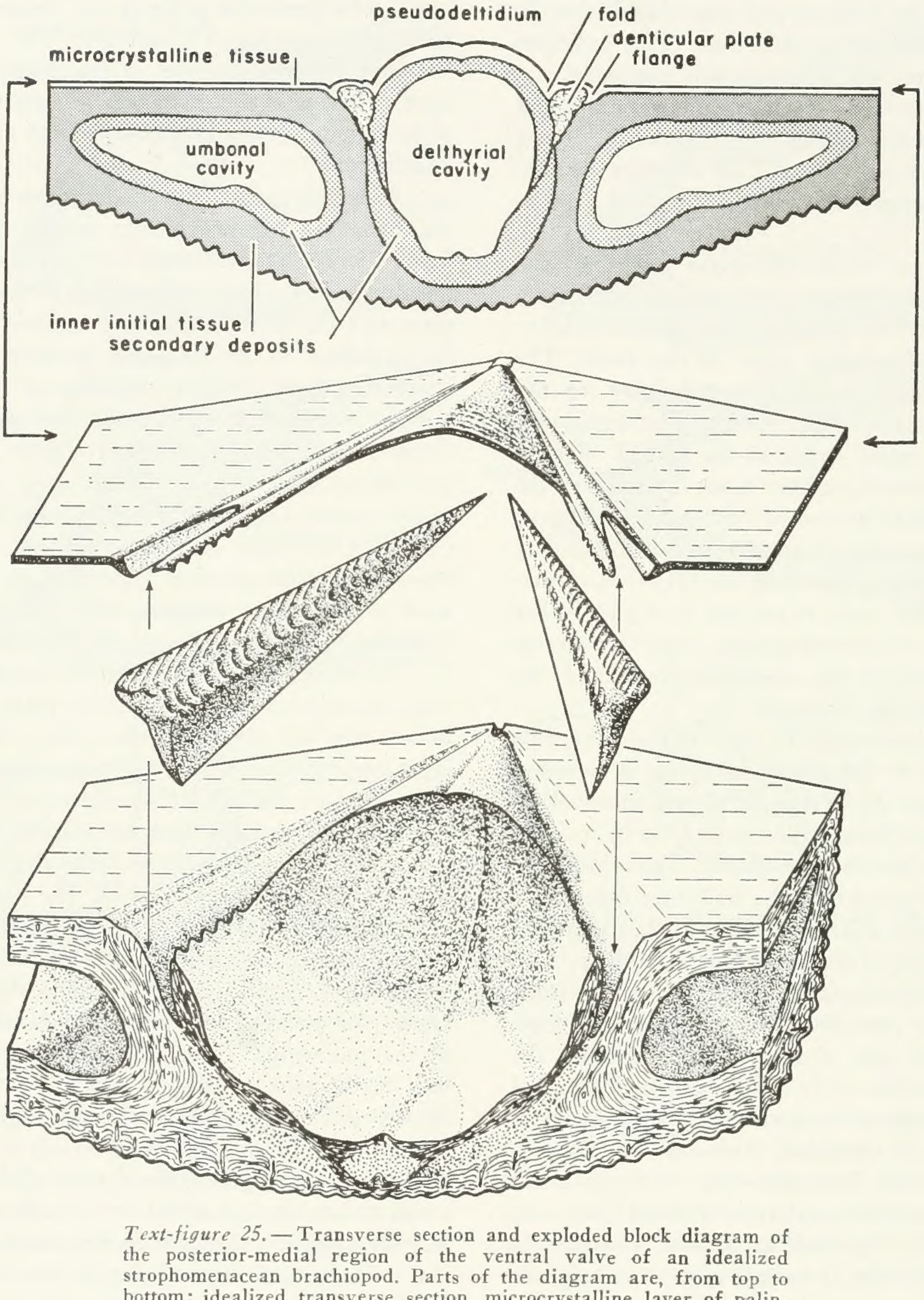
The base of the microcrystalline layer of the palintrope lateral to the denticular plate gives rise to a ridge or flange. This flange penetrates into the boundary between the lateral face of the denticular plate and its supporting dental lamella. The flange tends to be a curved triangle in cross section in specimens of *Oepikina, Rafinesquina, Kiaeromena, Strophomena,* and *Tetraphalerella. Tetraphalerella* possesses the largest and most sharply defined flange of the genera mentioned. *Holtedahlina sulcata* possesses a thickening in the ventral (fixed) surface of the microcrystalline layer which is less regular, shorter and wider than the flange of other species.

The flange does not occur along the entire anterior to posterior margin of the denticular plate. The flange, also, is absent along the lateral margin of the denticular plate to the anterior of the free edge (anterior edge) of the palintrope. The denticular plate is not apparent in sections less than approximately 0.8 mm from the apex of the valve. Between the posterior end of the denticular plate and the apex of the valve, the flange, if actually present, merges with the microcrystalline tissue of the palintrope and pseudodeltidium.

A shallow groove may be found on the interarea above the flange of microcrystalline tissue, as shown in Text-figure 26. The groove seems to be caused by folding of the microcrystalline layer downward between the denticular plate and the dental lamella. A groove has been observed in specimens of *Rafinesquina ponderosa* Ulrich, *Rafinesquina loxorhytis* (Meek), *Oepikina speciosa* Cooper, *Rhipidomena tennesseensis* (Willard), *Dactylogonia sculpturata* Cooper, *Dactylogonia alternata* Cooper, and *Strophomena grandimusculosa* Cooper. Observation of a groove in so many species suggests that the flange is a persistent feature of Ordovician strophomenaceans, though poorly developed in some species. Extension of the groove to the apex of the valve suggests that the flange does extend posterior to the extremity of the denticular plate.

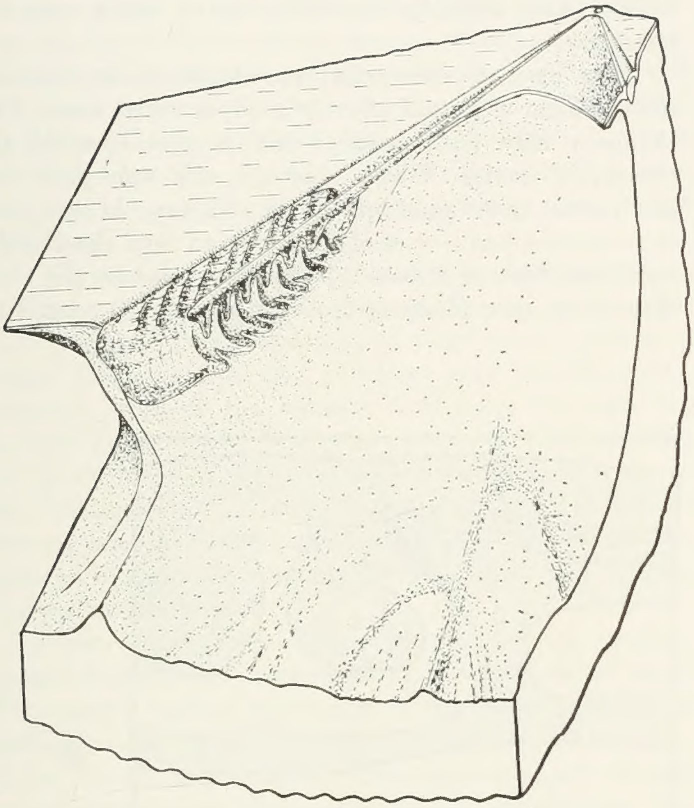
As noted, the microcrystalline layer of the palintrope may be arched over the denticular plate. Along the medial-dorsal edge of the denticular plate, the microcrystalline layer may project a short distance downward (ventrally) into tissue on the side of the delthyrial cavity. The microcrystalline layer folds back upon itself, returns to the surface where it arches over to form the pseudodeltidium, as shown in Text-figures 25 and 26. The isoclinal folding of the microcrystalline layer along the margin of the pseudodeltidium produces an optical effect in some peel sections in which there appears to be a sharply defined boundary between the pseudodeltidium and the microcrystalline layer of the palintrope. Hasty inspection of such sections may lead to the false conclusion that the microcrystalline layer of the palintrope and the pseudodeltidium are separate structures.

The boundary between the pseudodeltidium and palintrope commonly is marked by a shallow groove where the microcrystalline tissue is depressed down into the fold along the medial-dorsal edge of the denticular plate. Less commonly, a narrow ridge is the external expression of the fold. The latter condition is observed on species of *Rafinesquina.* The fold may be traced along the medial-dorsal edge of the denticular plate beyond the anterior margin (free margin) of the pseudodeltidium. The fold anterior to the free margin of the pseudodeltidium is set onto a chamfer along the



*Text-figure 25.*—Transverse section and exploded block diagram of the posterior-medial region of the ventral valve of an idealized strophomenacean brachiopod. Parts of the diagram are, from top to bottom: idealized transverse section, microcrystalline layer of palintrope and pseudodeltidium, two denticular plates, the remaining inner initial tissue and secondary deposits of the posterior-medial region.

The edges of lamellae adjacent to taleolae should curve toward the interior of the valve, not toward the exterior as shown in the lower drawing.



*Text-figure 26.*—The tooth, pseudodeltidium and adjacent structures of an idealized strophomenacean brachiopod. The dorsal and medial surfaces of the tooth are ridged by semidenticles. Microcrystalline and secondary tissues lap into the depressions between the semidenticles on the medial face of the tooth.

medial-dorsal edge of the denticular plate. In this position, the fold has the form of a ridge along the edge of the denticular plate. This anterior extension of the fold continues as a ridge almost to the anterior end of the tooth, as shown in Text-figure 26.

The ridge of microcrystalline tissue along the chamfered edge of the denticular plate overhangs the delthyrial cavity further than any other part of the tooth. The ridge occupies the undercut cavity of the sockets. This ridge acts as the pin of a hinge to positively lock the valves together. The ridged or semidenticulate dorsal-anterior and medial faces of the denticular plate are the bearing surfaces of the tooth which are in actual contact with the socket. The microcrystalline ridge along the dorsal-medial edge of the denticular plate has no bearing function. Scallops from the margin of the microcrystalline ridge may lie in the depressions between the semidenticles of the denticular plate, as shown in Text-figure 26.

The region of the interarea of Ordovician strophomenaceans which overlies the denticular plate is not homologous to the perideltidial area of orthotetaceans. The region is not so evident as the perideltidial area of orthotetids; it is topographically less distinct, narrower and not distinguished by features of prosopon. Sections of *Derbyia hooserensis* Dunbar and Condra show that the perideltidial area overlies the entire dental lamella and tooth-plate assembly and that the perideltidial area is simply a region of thinner microcrystalline tissue than that which covers the rest of the palintrope. The tooth-plate of *Derbyia* is taleolate, but denticles are not present along its surface. Consequently, this structure cannot be called a denticular plate. The denticular plates of strophomenaceans and the tooth-plate of orthotetaceans are similar in other respects and are probably homologous structures.

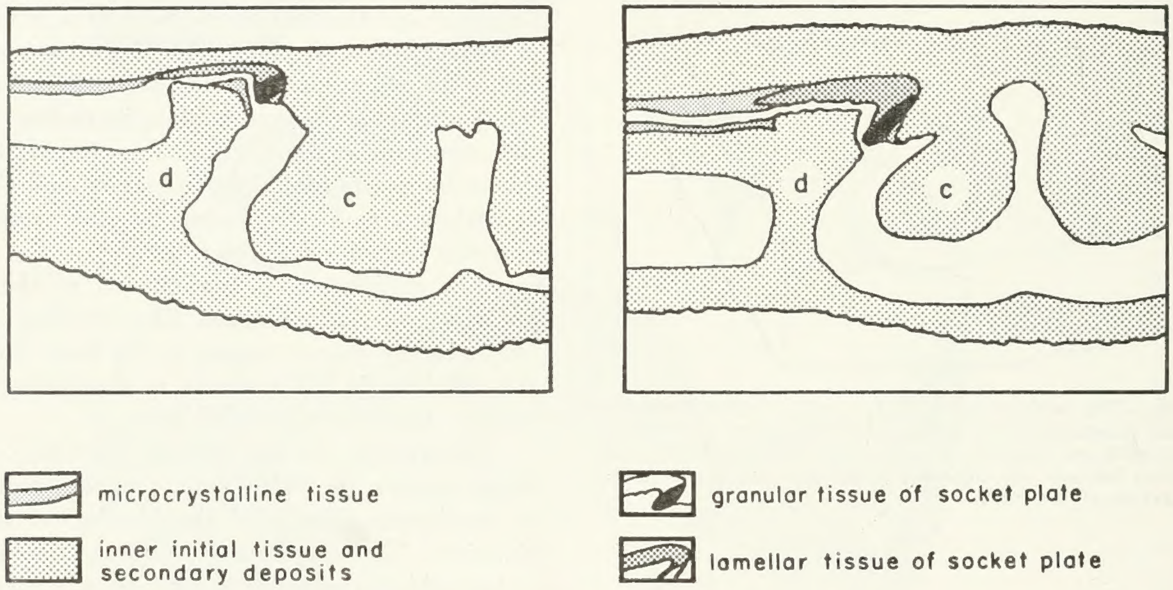
The chilidium is a continuation of the microcrystalline tissue of the palintrope. The chilidium is not backed by secondary deposit except at its base. For this reason, the chilidium is less resistant to mechanical abrasion and fracture than the pseudodeltidium.

Observation of the chilidia of entire specimens of many species of Ordovician strophomenaceans leads to an ambiguous opinion of the histological affinity of the chilidium. The chilidium of some specimens arises from a sheet which is attached to the inner margin of the sockets. Other specimens show unmistakable continuity of tissue from the interarea to the chilidium posterior to the sockets. Still other specimens possess a low ridge or groove along the margin of the chilidium posterior to the sockets which separates the chilidium from the interarea.

Serial transverse peel-sections permit a unified explanation for the conflicting observations. The socket is basically a groove in the inner initial tissue. A concave socket plate stretches across the floor and the medial margin of the socket, Text-figure 27. Flanges of microcrystalline tissue of the palintrope are inserted into the suture along the lateral and medial margins of the socket plate. The socket plate is covered by microcrystalline tissue posterior to the area where the socket is functional. Hence, the anterior margin of the chilidium nearest the sockets does arise from tissue of the medial margin of the sockets; the posterior apex of the chilidium does arise from microcrystalline tissue of the palintrope. The ridge or groove in the interarea along the margin of the chilidium posterior to the sockets marks the position of the microcrystalline tissue which fills in the posterior extremity of the socket. Microcrystalline tissue may extend from the medial margin of the sockets to the lateral bases of the cardinal process lobes.

The pedicle tube or collar of the juvenile *Rafinesquina* and *Strophomena* is found imbedded in inner initial tissue in the apex of the ventral valve of adult specimens. The pedicle tube is microstructurally identical to the pseudodeltidium. The thin, juvenile foramen of these genera is blocked with coarsely crystalline calcite which may be secondary.

The apex of the conical notothyrial cavity beneath the chilidium is formed entirely in inner initial tissue. The chilidium may be unusually thin at the apex of the notothyrial cavity. Where observed, this thin point lies just ventral to the basal bulb of the chilidium. In specimens of an undescribed species of *Rafinesquina* from the Cynthiana Formation of Kentucky, this thin point in the chilidium is an open foramen, probably secondarily opened by


d
c
d
c
microcrystalline tissue
inner initial tissue and secondary deposits
granular tissue of socket plate
lamellar tissue of socket plate

*Text-figure 27.* — Transverse sections through the tooth and socket of *Rafinesquina ponderosa* Ulrich (left) and *Strophomena planumbona* (Hall) (right) to show the structure of the socket plate. Inner initial tissue, secondary deposits, and denticular plate tissue are not differentiated; c — cardinal process, d — dental lamella, and denticular plate.

abrasion, weathering, and preparation. These observations support Spjeldnaes' (1957, p. 51) contention of a juvenile dorsal foramen of unknown function. The basal bulb of the chilidium represents a dorsal pad associated with the dorsal foramen in the juvenile. No microcrystalline tissue is incorporated into the inner initial tissue of the dorsal apex, that is, no inwardly directed tube or collar was associated with the dorsal foramen. The dorsal foramen was not functional in adults. The inner initial tissue which internally closes the dorsal foramen is a later deposit. The dorsal foramen has not been found in transverse sections through the chilidium.

The medial sagittal grooves in the pseudodeltidium and chilidium possibly originate from folding of these structures into the dorsal and ventral foramina in a juvenile stage. The groove of the chilidium may rest upon the posterior edge of the meso-cardinal ridge between the cardinal process lobes. As a consequence, the medial groove of the chilidium may simply be attributed to draping of the chilidium into the cleft between the lobes. There is no microstructural discontinuity across the groove of the pseudodeltidium, nor does the groove provide any support to the pseudodeltidium.

*Inner initial layer.* — Most of the shell of strophomenoid brachiopods is composed of the inner initial layer. The external surface of the disc of the valves generally is formed in inner initial tissue; all of the important structures of the internal surface of the valves are composed of inner initial tissue or have their origin in inner initial tissue. The inner initial layer is composed of coarse and fine lamellae penetrated by pseudopuncta and taleolae. The lamellae are oriented obliquely at a low angle to the surface of the valves. If a lamella is traced in a sagittal section, the posterior edge of the lamella is nearest the external surface of the valve, the anterior edge is nearest the internal surface of the valve. Viewed in transverse section, the severed ends of lamellae are lenticular, curved or wavey and roughly concentric to the surfaces of the valve. Hobbs and Cloud (1942, p. 24) described this aspect of the lamellae as having "the appearance of 'cut and fill structure' in stream sands."

The inner initial layer of strophomenaceans is not composed of flattened, elongated fibers, as Hobbs and Cloud (1942) and others described for other groups of brachiopods. The lamellae are sheetlike or fanlike in form, that is, the lamellae are too broad to be called fibers. Contrary to the observations of Blockman (1908), Jackson (1912, 1918), and Leidhold (1922), reported in Hobbs and Cloud (1942, p. 24), details of the size, thickness, number, and inclination of the lamellae seem to have little taxonomic significance in reference to Ordovician strophomenaceans. The only characters of potential taxonomic significance ascribable to lamellae are the color and sheen of the valves. The dark gray color common to many *Rafinesquina, Leptaena* and their allies has been tentatively related to the outer carbonate layer of these forms. It is possible, also, that the dark color is caused by the thicker, more translucent, and more steeply inclined fine lamellae possessed by these genera relative to the lamellae of *Oepikina, Furcitella* and *Strophomena* which are light colored. The nacreous sheen of some species of the Furcitellini and Glyptomenini, *e.g. Mjoesina higginsportensis* (Foerste) (formerly *Strophomena higginsportensis* Foerste), approaches the sheen of the Devonian stropheodontacean *Pholidostrophia*. The fine lamellae of *Mjoesina* and *Holtedahlina* are extremely thin and lie nearly parallel to the external surface of the valves.

The external surfaces of strophomenoid brachiopods do not possess true varices inasmuch as the external surfaces are formed of inner initial tissue. The "varices", properly fila, that are observed are molds of the actual varices of the outer carbonate layer or the truncated edges of the lamellae of the inner initial tissue. These two types of fila may be difficult to differentiate on eroded or abraded specimens. Molds of the true varices generally cross costae without deflection; laminae are deflected as they cross the costa in the manner of truncated plunging anticlines and synclines.

The coarse lamellae vary in number from 5 to 20 across the thickness of a valve. They appear as alternately darker and lighter bands across the shell's thickness. They vary in number in different regions of one valve; they differ in number in the same region of two valves of one species. The coarse lamellae are observed in both thin sections and peel sections. Peel sections do not show large quantities of opaque grains in the darker, coarse lamellae. Consequently, the coarse lamellae are caused probably by preferred orientations of the submicroscopic crystalline bodies of which the valves are constructed. Williams (1956, p. 249) provided a possible explanation for the coarse lamellae in his discussion of the growth of *Mucrospirifer* (Devonian), where he noted that "the lamellae . . . were built up by slight shifts in the direction of growth . . . of the mantle edge . . ." Shifting of the direction of growth would cause changes of the preferred crystallographic orientation of the submicroscopic grains of which the lamellae are composed. This could cause different gray-values of adjacent coarse lamellae. The coarse lamellae resemble and are to be compared optically to the banding of moiré silk.

Each coarse lamella is composed of many fine lamellae. The fine lamellae are so thin that they may be clearly resolved only at magnifications of ×50 and greater. The fine lamellae in a transverse section near the center of a dorsal valve of *Rafinesquina ponderosa* Ulrich number about 285 per mm. The fine lamellae are alternating bands of thin, dark material and thicker, clear calcite. The thin, dark bands contain opaque or darkly colored bodies which are too small to identify. Williams (1956, p. 249) contended that these darker bands are composed of chitin, *i.e.* periostracum, incorporated onto the surface of each lamella at the time of its secretion at the margin of the mantle. As noted previously, the dark lamellae may be outer carbonate tissue.

The inner initial layer grew in thickness throughout the life of the strophomenacean. Very young strophomenoids lack most internal structures except the cardinal process, teeth and sockets. Valves of very young strophomenoids apparently lack the inner initial layer. Large, gerontic specimens possess valves which are much thicker and which have more accentuated internal features than smaller ephebic specimens. Thus, the inner initial layer is initial only at its base. No means have been discovered for differentiating original from secondary "inner initial tissue" in those regions where the entire layer is penetrated by pseudopuncta.

Selected regions, for example, most of the material of the cardinal process lobes, do not possess pseudopuncta and are considered to be constructed of secondary tissues. Otherwise, the microstructure of these regions resembles inner initial tissue. The cardinal process lobes of all strophomenaceans develop from thin, vertical blades in the juvenile. The several types of adult cardinal processes are all secondary modifications. The dorsal septa of *Oepikina, Dactylogonia* and *Strophomena* develop from ridges of the inner initial layer. The dorsal septa may be modified and heightened by secondary deposits. Some, but not all, sections show a distinct dark line or fracture situated under the diductor muscle scars. This dark line is parallel to laminae and may differentiate original and secondary inner initial tissue in the ventral valve.

The marginal diaphragm is composed of inner initial tissue penetrated throughout its entire thickness by prominent pseudopuncta. The fine lamellae of the marginal diaphragm are thicker than elsewhere in the valves. The fine lamellae of the marginal diaphragm and the diductor muscle bounding ridges tend to be turbulent. The marginal diaphragm and muscle bounding ridges differ in that the fine lamellae terminate on the anterior and lateral surfaces of the marginal diaphragm and upon the posterior and medial facing surfaces of the muscle ridges.

The denticular plate of the tooth is composed of turbulent inner initial tissue with coarse, tabular pseudopuncta. The suture between the denticular plate and the microcrystalline layer of the palintrope is unmistakable. Large, tabular pseudopuncta which project from the dorsal surface of the denticular plate may penetrate as pegs into the microcrystalline tissue. A suture separates the denticular plate from the dental lamella. The suture may be obscured in sections because both structures are composed of lamellar tissue and the suture is deeply crenulated. Crenulations of the suture between the denticular plate and dental lamella have a dorsal-ventral direction. Thus, the crenulations are seen in longitudinal sections only. The suture between the inner initial layer and microcrystalline layer of the palintrope lateral to the denticular plate may be crenulated, also. These crenulations cause the parallel, anterior to posterior grooves of the interareas. The microcrystalline flange lateral to the denticular plate, discontinuity of lamellae between the denticular plate and the dental lamella and differences of color and texture of the denticular plate in whole specimens of the ventral valve indicate that the denticular plate is a separate part.

The dental lamellae are continuous with the inner initial tissue of the floor of the valves and with the palintrope. No suture is evident at either junction. The fine lamellae of the inner initial tissue may be sharply flexed but not discontinuous at these two positions. The sharp flexure of the lamellae produces in transverse sections a line along the axis of the flexure as may be seen on the edge of a sharply folded magazine or booklet. This line in the flexure may be misinterpreted as a suture. Similar lines of flexure may be found at the cardinal extremities, where the inner initial tissue of the palintrope and floor of the valve meets, and under the lateral margins of the cardinal process lobes.

The socket is a groove in the inner initial tissue occupied by the compound socket plate. The socket plate is less distinctly delineated than the denticular plate. Some sections of a specimen may show a socket plate while adjacent sections may not. Thus, the reality of a socket plate is not positively confirmed.

The socket plate seems to be composed of a granular blade or rod along the medial margin of the socket, and a concave plate of dark, finely lamellar, coarsely pseudopunctate tissue on the floor of the socket, as shown in Text-figure 27. Lamellae of the concave plate may be either smooth or turbulent. Spjeldnaes (1957, text-figure 3) called only the granular blade the socket plate. As both pieces of the assembly are set apart from the inner initial tissue by a suture and the margins of the assembly are underlain by flanges of microcrystalline tissue of the palintrope, the granular blades and concave plate together constitute a compound socket plate.

The coarse pseudopuncta of the concave plate form endospines which mesh with the semidenticles of the dorsal surface of the denticular plate. The granular blade or rod is scalloped along the medial-ventral margin of the socket. The scallops, which do not seem to be formed by pseudopuncta, mesh with the ridges of the medial face of the denticular plate. The socket plate is thicker and better delineated in resupinate strophomenaceans, *e.g. Strophomena,* than in concavo-convex forms, *e.g. Rafinesquina, Kiaeromena* and *Oepikina.* In the latter forms, the concave plate is thin and the granular blade is a terete rod. The principal articulatory contact of concavo-convex species lies between the granular rod of the socket and the medial face of the denticular plate. The major articulatory contact of resupinate species is between the dorsal surface of the denticular plate and the floor of the socket. This may explain why the largest ridges of denticular plates are on the dorsal surface in resupinate forms and the medial surface in concavo-convex forms; why the denticular plate is exposed commonly on the interarea of resupinate forms but exposed rarely on the interarea of concavo-convex forms; and why the sockets of resupinate forms are wider than the sockets of concavo-convex forms.

The edges of the compound socket plate are underlain by flanges of microcrystalline tissue of the palintrope. In this respect, the socket plate and denticular plate have a similar relationship to the microcrystalline layer. Transverse sections through the sockets of the orthoid brachiopods, *Plaesiomys subquadrata* (Hall) and *Hebertella sinuata* (Hall) show structures comparable to the structures of the sockets of strophomenaceans. The bases of the brachiophores are granular rods inserted along the medial margins of the sockets. The floor of the socket is underlain by a concave lamellar plate, a recumbent fulcral plate. Possibly the strophomenacean socket buttress is a homologue of the orthoid brachiophore. Öpik (1933) advocated this conclusion with respect to the plectambonitaceans.

*Secondary deposits.* — Secondary deposits within strophomenacean brachiopods are concentrated toward the central-posterior region of the valves. Secondary deposits are associated with the following structures: the muscle bounding ridges, the medial and lateral dorsal ridges, the surface of the muscle scar areas, the posterior platform, the cardinal process lobes and meso-cardinal ridge, the lateral umbonal cavities and the delthyrial and notothyrial cavities. Secondary deposits are constructed of three distinct tissues which are morphologically segregated and which may have served different functions.

The first variety of secondary tissue resembles inner initial tissue except that pseudopuncta are rare to absent. This variety of secondary deposit is translucent in peel sections. It possesses fine laminae which may be continuations of the laminae of the inner initial layer. The second variety of secondary tissue has a microcrystalline structure. This type of tissue incorrectly has been called cryptocrystalline. The grains may be clearly resolved at ×50 magnification and, thus, are larger than the grains of the microcrystalline tissue of the palintrope. The result is that the microcrystalline secondary deposits are more translucent than the microcrystalline layer of the palintrope. The microcrystalline secondary tissue is associated mainly with sites of muscle attachment. The third variety of secondary tissue resembles the outer carbonate layer of the disc of the valves. This tissue is formed of thin lamellae with thick, dark boundaries. The tissue appears darker and denser than inner initial tissue or secondary lamellar tissue in peel sections. This dark lamellar secondary tissue is not pseudopunctate. This dark tissue is associated mainly with the muscle scar regions of the valves.

The relatively clear, lamellar secondary deposits are found in association with the muscle bounding ridges, the posterior platform, the cardinal process lobes, the lateral umbonal cavities and the delthyrial and notothyrial cavities. The lamellar secondary tissue is rarely pseudopunctate in the muscle bounding ridges, never pseudopunctate in other regions. In the muscle bounding ridges, the lamellae curve into the ridges such that the free ends of the lamellae are exposed on the posteriorly and medially directed surfaces of the ridges. This condition causes the muscle bounding ridges of transverse sections to resemble a breaking wave.

The laminae are parallel to the surfaces of the umbonal cavities in transverse sections so that the umbonal cavities appear as sets of concentric triangles. The ventral surface of the umbonal cavities may be interrupted by posterior extensions of the marginal diaphragm. These swellings of secondary tissue tend to divide each lateral umbonal cavity into two chambers. The internal surfaces of the pseudodeltidium and chilidium and the medially directed surfaces of the dental lamellae are coated with lamellar secondary tissue. The lamellae of the tissue are parallel to the internal surface of the inner initial layer or microcrystalline layer. Transverse sections through the delthyrial cavity and pseudodeltidium reveal the lamellae of the secondary tissue as a set of concentric circles or ovals. The pedicle conduit of *Leptaena richmondensis* Foerste lies in the center of the concentric lamellae. The pedicle conduit itself appears to be a thin microcrystalline tube. The pedicle conduit of species of strophomenaceans without a functional pedicle in adulthood, including species of *Oepikina, Rafinesquina, Strophomena,* and *Tetraphalerella,* is a microcrystalline tube with a coarsely crystalline plug of secondary tissue.

The posterior platform, the cardinal process lobes and the meso-cardinal ridge are constructed of clear lamellar secondary tissue. These lie upon a gently swollen area of inner initial tissue in the posterior central region of the dorsal valve. There is a low swelling of inner initial tissue under each cardinal process lobe. The swellings do not have the shape, the angularity or the topographic relief of the cardinal process lobes as shown in Text-figure 28.

The tissue of the posterior platform, cardinal process lobes, and meso-cardinal ridge, viewed in peel section, is the clearest encountered anywhere in the brachiopod. The fine lamellae are thicker than usual and the dark planes separating the fine lamellae are thin. There are no pseudopuncta in the secondary tissue of the notothyrial platform or cardinal process lobes. Neverthless, there is no distinct line of demarkation between the inner initial tissue and these structures.

The posterior surfaces of the cardinal process lobes are the sites of insertion of the diductor muscles. These myophore surfaces bear deep grooves which are arranged as radii from the apex of the valve. The radial grooves seem to correspond to radially arranged planes within the tissue of the cardinal process lobes. The radial planes cross and interrupt the turbulent lamellae of the secondary tissue. This condition imparts a cellular or cancellus appearance to sections through the tissues of the myophore regions. The structure of the cancellus tissue of the myophores resembles bone. The cancellus appearance of the myophores is shown in Text-figure 28.

A meso-cardinal ridge or septum occurs in most strophomenacean species, Text-figure 28. The meso-cardinal ridge may be evident on the internal surface or may be buried in overhanging or confluent tissue of the medial sides of the cardinal process lobes. The meso-cardinal ridge has been the subject of considerable speculation. If the meso-cardinal ridge and the cardinal process lobes have the same origin, the bifid cardinal process of the Strophomenacea then could be compared with confidence to the trifid cardinal process of the Plectambonitacea.

The meso-cardinal ridge overlies the posterior extension of the medial ridge from the viseral cavity surface of the dorsal valve. The medial ridge may project under the posterior platform and between the bases of the cardinal process lobes. The meso-cardinal ridge and underlying medial ridge are separated commonly by a zone of lamellar secondary tissue comparable in thickness to the thickness of the posterior platform. The lamellae of this zone of secondary tissue are not folded into the base of the meso-cardinal ridge but they are folded into the bases of the cardinal process lobes. The meso-cardinal ridge is a gerontic feature; it is not present in the ephebic brachiopod. The meso-cardinal ridge is a superficial structure of minor phylogenetic significance.

The clear, lamellar secondary tissue which is found in many other regions of the valves seems to be a filling substance with little function other than to strengthen the valves by increasing thickness, to fill in pockets and holes and to buttress ridges.

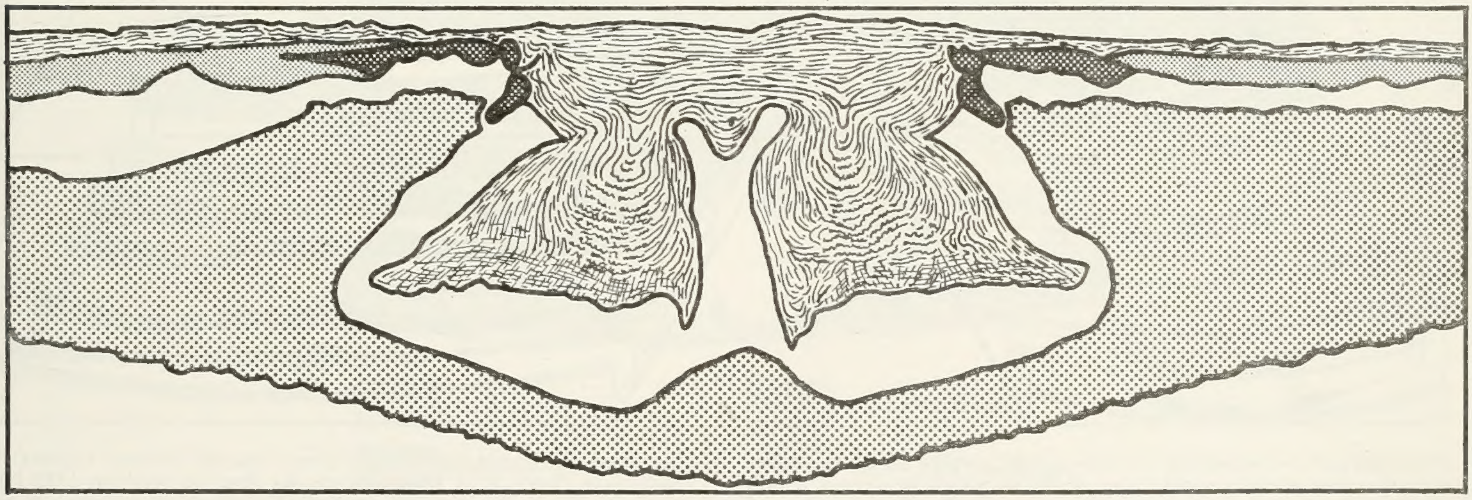
The secondary deposits of the muscle scar areas of the dorsal and ventral valves are constructed of layers of microcrystalline and dark lamellar tissue. Specimens of all species of strophomenaceans that have been sectioned, except *Dactylogonia alternata* Cooper, show layers of the microcrystalline and dark lamellar secondary deposits in the same sequence and of generally similar shape.

The microcrystalline and dark lamellar secondary deposits of the posterior-central region of the ventral valve of *Rafinesquina ponderosa* Ulrich and of the dorsal valve of *Tetraphalerella neglecta* (James) are shown in Text-figure 29. In the anterior-central region of the ventral valve of *Rafinesquina ponderosa* Ulrich (see first section of the text-figure), the inner initial tissue is overlain by a broad expanse of microcrystalline secondary tissue (unpatterned zone of diagram). The central region of the microcrystalline tissue is depressed and replaced by a transversely curved plate of dark lamellar tissue (black plate). The central region of the curved plate of dark lamellar tissue is overlain by microcrystalline tissue (unpatterned area). These three layers are interpreted as follows: the lower layer of microcrystalline tissue is the site of diductor muscle attachment;

the upper layer of microcrystalline tissue is the site of adductor muscle attachment; the dark plate marks the position of attachment of connective tissue. As the brachiopod grew in length and width, the area of attachment of the adductor muscles became wider and migrated toward the anterior. The tendons on the surface of the adductor muscles spread laterally with growth and increased shell thickness with the result that tissue marking the site of tendon attachment forms a curved plate. Succeeding sections toward the posterior (sections 4 to 11) show introduction of a partition of dark lamellar tissue into the center of the microcrystalline tissue underlying the adductor scars. This partition is evidence of separation of the adductor muscles and insertion of a tendinous strip between them. Toward the posterior, the dark lamellar tissue spreads laterally across the microcrystalline tissue of the diductor muscle scars, fifth section, and centrally across the microcrystalline tissue of the adductor muscle scars, sixth section. The lateral and central spreading of the dark lamellar tissue marks the posterior margin of the diductor and adductor muscles at the time of death of the brachiopod. The spreading of the dark lamellar layer over the adductor muscle scars occurs directly beneath the anterior edge of the cardinal process lobes. Posterior extensions of the microcrystalline layers under dark lamellar tissue mark former positions of diductor and adductor muscle attachment. These posterior sites of attachment were abandoned during growth as the posterior margin of the muscles migrated toward the anterior.

The microcrystalline and dark lamellar secondary tissues from the muscle scars may be traced into the delthyrial cavity. The medial body of microcrystalline tissue from the adductor muscle scars disappears under the delthyrial cavity. The microcrystalline layer from the diductor muscle scars becomes a thin plate in the floor of the delthyrial cavity. The lateral edges of this plate curve up the sides of the dental lamellae and contact the basal edge (ventral edge) of the denticular plate. In a few sections, the entire denticular plate seems to be bedded in this tissue. Further toward the delthyrial apex, this layer becomes thinner and finally disappears. In Text-figure 30, the plate of secondary tissue in the floor of the delthyrial cavity is this microcrystalline tissue. Note that the plate thins in sections A to E and is absent from section F, possibly because of abrasion.

The dark lamellar secondary tissue may be traced into the delthyrial cavity. At the anterior end of the delthyrial cavity, the dark lamellar secondary tissue curves up the sides of the dental lamellae. Toward the apex of the delthyrial cavity, the dark lamellar secondary tissue is restricted to a medial position and either gradually disappears, as in

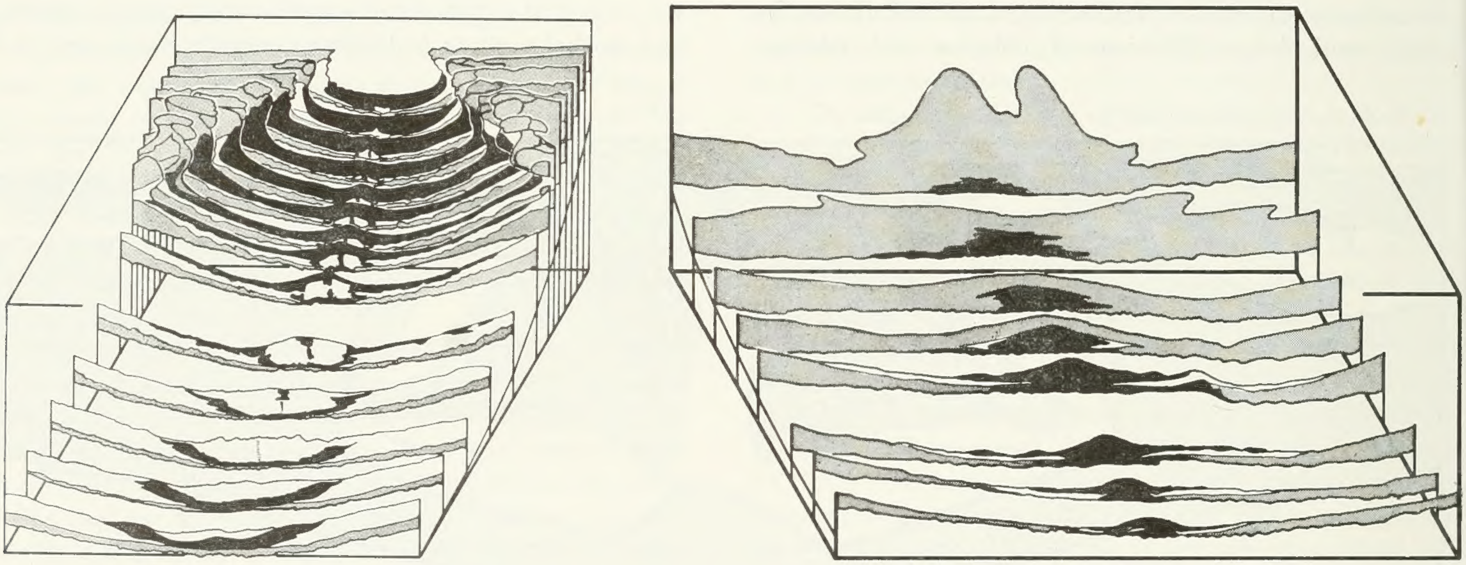


*Text-figure 28.* — The microstructure of the cardinal process lobes and meso-cardinal ridge of *Rafinesquina ponderosa* Ulrich. The configuration of the lamellae of the secondary tissue of the cardinal process lobes and meso-cardinal ridge suggests that the meso-cardinal ridge develops later in ontogeny than do the lobes. Other tissues of the dorsal valve include the cancellus tissue of the myophores of the cardinal process lobes (cross-hatched), the socket plates (coarse stipple) and the microcrystalline layer of the palintrope (fine stipple). The ventral valve is shown for reference only; its tissues are not differentiated. Magnification about ×10.

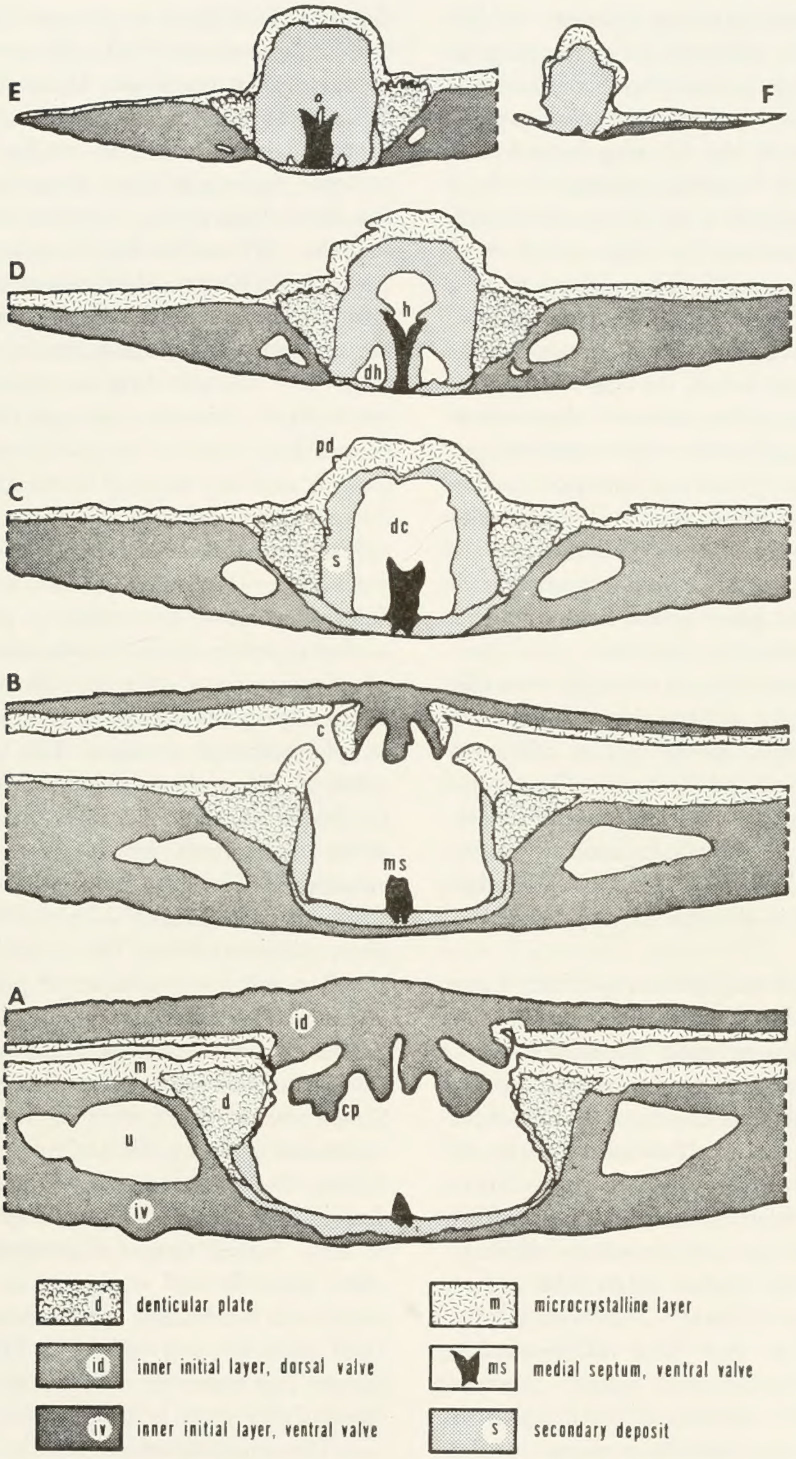
*Rafinesquina ponderosa* Ulrich, or becomes compressed into a medial septum, as in *Strophomena vetusta* (James), Text-figures 29 and 30.

The microcrystalline and dark lamellar secondary tissues are submerged under a layer of clear lamellar secondary tissue in the delthyrial cavity. This clear lamellar layer begins on the sides of the dental lamellae below the exposed medial faces of the denticular plate. It is not known whether clear lamellar tissue or dark lamellar tissue flows into the depressions between the semidenticles of the medial face of the denticular plate as shown in Text-figure 26. The clear, lamellar secondary deposit becomes thicker toward the delthyrial apex. Under the pseudodeltidium, this tissue covers all surfaces of the delthyrial cavity. Horizontal or vertical transverse flanges in the surface of this tissue at the delthyrial apex of some species, *e.g. Strophomena concordensis* Foerste, may mark the site of attachment of adjustor or pedicle muscles.

The delthyrial regions of *Strophomena vetusta* (James) and *S. planumbona* (Hall) differ from the delthyrial regions of all other strophomenaceans that have been sectioned, including other species of *Strophomena*. In these two species, the dark lamellar secondary tissue of the delthyrial region becomes concentrated into a thin, sharp septum. The septum has a rounded top in *S. planumbona* (Hall) and a flattened or troughlike top in *S. vetusta* (James), see Text-figure 30. The septum is found to the tip of the delthyrial cavity. There is a hole in the clear, lamellar secondary tissue on either side of the septum. The holes are directed into the apex of the ventral valve. These holes are filled with coarsely granular, sparry calcite which was deposited after death. *Tetraphalerella neglecta* (James) has a pair of cavities in the floor of the delthyrial cavity which receive the posterior ends of the cardinal process lobes when the valves are closed. This is not the function of the pair of cavities in *S. vetusta* (James) or *S. planumbona* (Hall). No other strophomenacean species that has been sectioned has a pair of cavities in the floor of the delthyrial cavity, however, sections of the delthyrial region of *Thaerodonta rugosa* (Meek), a plectambonitacean, reveal a pair of holes in the secondary tissue. The pairs of holes in the delthyrial regions of *Thaerodonta* and *Strophomena* have no taxonomic significance,



*Text-figure 29.* — Assembled transverse serial sections of the posterior-central region of the ventral valve of *Rafinesquina ponderosa* Ulrich (left) and of the posterior-central region of the dorsal valve of *Tetraphalerella neglecta* (James) (right). Tissues shown: black — dark, finely lamellar secondary tissue; white — microcrystalline tissue; stippled — inner initial tissue and clear secondary tissue. The curved lines along the sides of the blocks are a projection of the curvature of the mid-line of the valves. Interval between sections: *R. ponderosa* (left), 1/16 inch between the first six sections, 1/32 inch between sections six and seven, 1/64 inch between remaining sections; *T. neglecta* (right), 1/32 inch between all sections except sections three and four which are 3/64 inch apart. Magnification: left ×4.6, right ×5.5.


E
F
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B
c
ms
A
id
m
d
cp
u
iv
d denticular plate
m microcrystalline layer
id inner initial layer, dorsal valve
ms medial septum, ventral valve
iv inner initial layer, ventral valve
s secondary deposit

*Text-figure 30.*—Transverse serial sections of the posterior-central region of *Strophomena vetusta* (James); c — chilidium, cp — cardinal process, dc — delthyrial cavity, dh — cavity in secondary tissue which fills apex of delthyrial cavity, h — hemisyrinx, pd — pseudodeltidium, u — umbonal cavity. Interval between sections: A to B, 1/32 inch; remaining sections, 1/64 inch; section F less than 1/64 inch from posterior end of valve. Magnification ×6.1.

but they may indicate the presence of an unknown fleshy structure. The pair of apically directed holes flanking a septum with a trough-shaped top, as borne by *Strophomena vetusta* (James), has an interesting similarity to the spondylium triplex and hemisyrinx of the pseudopunctate clitambonitoids of the superfamily Gonambonitacea.

The secondary deposits associated with the muscle scars of the dorsal valve are not so complex as those of the ventral valve, as shown in Text-figure 29. The regions of adductor muscle attachment are underlain by coarsely microcrystalline tissue. A ridge of dark inner initial tissue, which is the medial ridge of the dorsal valve, divides the microcrystalline tissue. The microcrystalline tissue of the central region of most species is spread across the medial ridge. Posterior to the center of the valves, just anterior to the anterior margin of the posterior platform, a ridge of dark, lamellar secondary tissue appears on top of the medial ridge. The two superimposed ridges are commonly separated by a thin zone of clear, lamellar inner initial tissue. At the anterior margin of the notothyrial platform, the dark lamellar ridge of secondary tissue spreads laterally over the microcrystalline layer. This region of lateral spreading corresponds to the posterior margin of the dorsal adductor muscle scars. The microcrystalline and dark, lamellar secondary tissues can be traced under the cardinal process. Under the cardinal process, lamellae of the dark, lamellar tissue gradually become thicker and clearer. The medial ridge grades into clear lamellar tissue in the posterior region of the notothyrial platform.

Specimens of *Stropheodonta* (Devonian) that have been sectioned possess secondary tissue deposits in the muscle scar regions that strongly resemble those of *Rafinesquina.* In fact, sections of these two genera cannot be differentiated easily without reference to the teeth and cardinal processes. The plectambonitacean *Thaerodonta rugosa* (Meek) possesses a layer of microcrystalline tissue overlain by a curved plate of dark lamellar tissue in the ventral valve. There is no differentiation of secondary deposits in the muscle scar regions of the dorsal valve. The orthotetaceans *Fardenia subplana* (Conrad) (Silurian) and *Schuchertella sp.* (Devonian) do not show differentiation of secondary tissue in the muscle scar region. *Derbyia hooserensis* Dunbar and Condra shows a differentiation of microgranular and dark lamellar secondary tissue in the muscle scar regions of the ventral valve. The high medial septum is constructed of dark lamellar tissue. The adductor muscle scar areas of the dorsal valve do not show secondary deposits. Transverse sections of the orthoid species *Plaesiomys subquadrata* (Hall), *Hebertella sinuata* (Hall), and *Platystrophia acutilirata* (Conrad) show microstructurally differentiable tissue associated with the muscle scars of the ventral valve. The tissues of the muscle scar areas of these orthoids have not been examined in detail. Nevertheless, the tissue layers seem to have the same general form and sequence as found in strophomenaceans.

*Microstructure of the dorsal ridges.* — The ridges of the internal surface of the dorsal valves of strophomenaceans are not conspicuous features in thin or peel sections. The ridges are most evident on specimens of the older genera, for example, *Dactylogonia* and *Oepikina.* The ridges appear in modified form in *Strophomena, Holtedahlina,* and allied genera and are greatly reduced to absent in *Leptaena, Rafinesquina,* and related genera. The dorsal ridges are significant in the evolutionary history of the superfamily Strophomenacea and may become important structures for determination of the ancestry of the strophomenaceans within the superfamily Plectambonitacea.

Specimens of the plectambonitacean species *Thaerodonta rugosa* (Meek) have been sectioned for comparison to strophomenacean sections. The inner surface of the dorsal valve of *Thaerodonta rugosa* (Meek) possesses seven septa (a medial septum and three pairs of lateral septa) which invite comparison to the five dorsal ridges of strophomenaceans. The shell material of the dorsal valve of *Thaerodonta rugosa* (Meek) does not resemble the shell material of strophomenaceans. The inner initial layer is thin, poorly lamellar and has a cellular or prismatic appearance in peel sections. The difference in appearance of the tissue is not caused by preservation. The specimens of *Thaerodonta* came from the same outcrop as several of the specimens of *Strophomena* which were sectioned. The medial septum is composed of dark, prismatic to poorly lamellar inner initial tissue. The anterior pair of lateral dorsal septa, the anderidia, are thin and high. They possess a thin axial plate of inner initial tissue of prismatic appearance. The axial plate expands and contracts in transverse section, which imparts to it a beaded appearance. The lateral flanks of each axial plate are covered by a fillet of prismatic secondary tissue. The two pairs of low, posterior septa are composed of relatively clear prismatic tissue without axial structures.

The microstructure of the dorsal ridges of *Oepikina gregaria* Cooper, *O. minnesotensis* (Winchell), and *Dactylogonia alternata* Cooper cannot be compared in all aspects to the septa of *Thaerodonta rugosa* (Meek). *Oepikina* and

*Dactylogonia* do not possess any tissue with a cellular or prismatic appearance except in the cardinal processes. The medial and anterior pair of dorsal ridges of *Oepikina* and *Dactylogonia* are linear welts of dark, finely lamellar inner initial tissue containing pseudopuncta. There is no indication in the ridges of either genus of an axial plate but there is a cylindrical core of granular tissue at the anterior ends of the medial ridge and anterior-lateral ridges. The core of granular tissue in the anterior pair of ridges of *Oepikina* and *Dactylogonia* may be homologous to the axial plates in the anterior pair of septa of *Thaerodonta.* This comparison leaves the granular core in the medial ridge of *Oepikina* and *Dactylogonia* without a comparable feature in *Thaerodonta.* The medial septum of *Thaerodonta* disappears anterior to the posterior platform. The axial plates of the anterior pair of septa of *Thaerodonta* converge and unite at the anterior margin of the posterior platform. This union produces a "U" shaped plate filled with secondary tissue. The medial and anterior pair of ridges of *Oepikina* coalesce into a single medial ridge near the anterior margin of the posterior platform. The pair of posterior-lateral ridges of *Oepikina* and *Dactylogonia* differ from the other ridges by being composed of clearer, more coarsely lamellar tissue identical to normal inner initial tissue. As noted, the posterior pair of dorsal ridges are less persistent in the phylogeny of the Strophomenacea than either the anterior pair of dorsal ridges or the medial ridge. The single pair of posterior-lateral ridges of *Oepikina* and *Dactylogonia* and the dual pairs of posterior-lateral septa of *Thaerodonta* are simple muscle bounding ridges, *i.e.* transmuscle ridges.

Specimens of all genera of strophomenaceans that have been sectioned possess a medial ridge composed of dark, finely lamellar inner initial tissue. In this character, all genera resemble *Oepikina* and *Dactylogonia. Holtedahlina* and *Oepikina* possess a medial ridge with a cylindrical core of granular tissue, but *Strophomena, Tetraphalerella, Rafinesquina,* and *Kiaeromena* do not. The cylindrical core of granular tissue probably forms the breviseptum.

The lateral pairs of dorsal ridges of *Holtedahlina* and *Oepikina* are similar in microstructure. Species of *Strophomena* show three types of ridges in the dorsal valve. The anterior pair of ridges of *S. nutans* Meek resemble the dorsal ridges of *Oepikina* by being linear welts of inner initial tissue. These ridges of *S. nutans* Meek are wider and are composed of clearer, more coarsely lamellar tissue than the dorsal ridges of *Oepikina.* The lateral ridges of *S. nutans* Meek are buried beneath secondary tissue in the posterior platform region. *S. planumbona* (Hall) possesses lateral ridges composed of dark, lamellar secondary tissue resembling the tissue adjacent to the muscle scars of the ventral valve. The dark tissue of the lateral ridges overlies clear, pseudopunctate, inner initial tissue and, hence must be a secondary deposit. *S. vetusta* (James) possesses many irregularly formed lateral dorsal ridges. These are constructed of coarsely lamellar, coarsely taleolate, clear inner initial tissue. The ridges of *S. vetusta* (James) have topographic relief but are not microstructurally differentiated. *Tetraphalerella neglecta* (James), *Rafinesquina ponderosa* Ulrich, *Leptaena richmondensis* Foerste, and *Megamyonia unicostata* (Meek and Worthen) do not possess lateral ridges on the internal surface of their valves or in the microstructure tissue of their valves. The ridges of *Strophomena* which are composed of secondary tissue are not related to the ridges of *Oepikina* which are composed of inner initial tissue. The ridges of *Strophomena* should be called adventitious ridges because of their irregular form, inconsistent occurrence and secondary character.

There is no consistency of construction of the dorsal ridges throughout the superfamily Strophomenacea except for the ubiquitous medial ridge. The pairs of lateral dorsal ridges are a phylogenetically primitive feature which are suppressed and even deleted in advanced lineages.

*Pseudopuncta and taleolae.* — The most convenient unifying character of the strophomenoid brachiopods is the pseudopunctate condition of the shell material. Williams (1956, p. 251) proposed the term "taleolae" for the slender rods of granular calcite which occur along the axes of localized deflections of the lamellae of the shell material, the pseudopuncta. His definitions of that date left unclear the difference between a pseudopunctum and a taleola. The distinction between these structures was resolved in the *Treatise on Invertebrate Paleontology, Part H,* 1965, page 151. The present observations largely support Williams' (1956, p. 251; 1953, p. 3) descriptions of pseudopuncta and taleolae without serious conflict.

Taleolae are thin unbranched rods of granular calcite which arise from an indistinct, expanded base at, or just below, the outer surface of the inner initial layer. The taleolae are crossed by dark lines which suggest the presence of cleavages or grain boundaries. Taleolae commonly penetrate to the interior surface of the inner initial layer. They may project into the visceral cavity as short spines called endospines. Some taleolae do not seem to penetrate the entire inner initial layer but this trait cannot be established without question because sections may cut obliquely through taleolae.

Taleolae may be straight or gently curved in sagittal section. They most commonly curve or slope slightly to the anterior of a line perpendicular to the shell surface when they are traced from exterior to interior. Some taleolae may be oriented at random angles to the shell surface and may even curve in a vermicular fashion. Randomly oriented and vermicular taleolae are found only in thickened regions of the inner initial layer where the lamellae are turbulent, as in the muscle bounding ridge and the marginal diaphragm.

The lamellae of the inner initial layer adjacent to taleolae are curved toward the internal surface of the valve. This curvature produces the illusion that the taleolae have been pressed through the inner initial tissue as pins might be pressed through a magazine. The width of the zone of curvature of the lamellae around a taleola is about one to one and a half times the diameter of the taleola. Curvature of the lamellae to form a pseudopunctum amounts to approximately 45 degrees rotation. There is slightly more than 45 degrees curvature of lamellae along the anterior margin of a taleola and from 30 to 45 degrees curvature along the posterior margin. Variation of curvature is caused by the anterior slope of the taleolae. The set of stacked cones of lamellae, *i.e.* a pseudopunctum, may occur without an axial taleola, but a taleola never occurs without deflected lamellae around its margin.

The margin of a taleola may be deeply indented by the edges of the lamellae. The indentations may be so deep as to cause a taleola to have a beaded appearance in thin sections. Rarely, lamellae pass through a taleola without interruption. Cleavages or grain boundaries in taleolae commonly correspond to adjacent lamellae, hence, may not be crystallographically controlled. Some taleolae have smooth, uninterrupted margins. Those with uninterrupted margins have a thin, dark layer which separates the taleola from the edges of adjacent lamellae. This layer has the same appearance as the thin dark layers which separate lamellae. The dark, marginal layer of taleolae is not visible in peel sections. Williams (1956) described "two or more layers" around the central axis of some taleolae and Muir-Wood (1965) reported a central cavity within taleolae. Two layers may be observed in cross sections of large taleolae of *Leptaena richmondensis* Foerste and *Megamyonia unicostata* (Meek and Worthen). The outer layer is probably the upturned edge of a lamella and not a layer of the granular rod of a taleola. No evidence of a central cavity can be found in the taleolae of strophomenaceans.

No evidence has been found to support Spjeldnaes' (1957) belief that taleolae were puncta during the life of the brachiopod and were filled by post-depositional precipitation of sparry calcite. Spjeldnaes based his theory upon the presence of "possible traces of clay material" (1957, p. 10) in taleolae of one sectioned specimen of *Leptaena depressa* (Sowerby) and upon depressions in the crests of endospines. In 1929, Kozłowski presented convincing evidence that pseudopuncta are structures of the original shell material.

Foreign matter is commonly observed in sections of brachiopods. Some enters by inadequate cleaning of sections prior to mounting; some enters along natural fractures in shells. "Pearls" formed by deposition of secondary shell tissue over pockets of clay and fossil fragments have been observed. A specimen of *Rafinesquina* incrusted by *Lichenocrinus* (a crinoid radix) shows deep erosion and entrapment of foreign matter under the margin of the crinoid base. The canals of *Rhopalonaria* (a bryozoan) on a sectioned specimen are filled with clay. Sections of *Leptaena* and *Rafinesquina* usually show tiny vermicular tubes in the inner initial layer. These have the dimensions of dalmanelloid endopuncta. They do not appear to be true puncta because they have an erratic distribution within the shell material, some specimens lack tubes, the tubes are randomly curved and branched, the tubes seem to emerge at both the exterior and interior surfaces of the shell and no brush can be found at the external end of the tubes, as occurs at the external end of endopuncta. These tubes are filled with an opaque substance which makes them conspicuous. One tube penetrates diagonally through a taleola. The tubes are probably caused by an epizooic (or epiphytic) microorganism. Regardless of the origin of the tubes, they do introduce foreign matter into the shells. Specimens of the dalmanelloid *Onniella meeki* (Miller) from the Waynesville Formation, Upper Ordovician, Ohio, commonly show euhedral crystals of pyrite in the endopuncta. Associated specimens of *Rafinesquina ponderosa* Ulrich and *R. loxorhytis* (Meek) do not have pyrite along the axes of the pseudopuncta.

Pits rarely occur on the crests of unweather endospines. Etching by acid proceeds more rapidly in granular tissue of taleolae than in the surrounding lamellar tissue of the pseudopuncta. The result is a pit in the crest of endospines that have been subjected to gentle, natural or laboratory etching.

No taleolae resembling the "hemispherical humps" described by Williams (1956, p. 251) were observed. Toward the margins of shells, especially in the marginal diaphragm, there commonly are broad, hemispherical swellings in the lamellar tissue which have the appearance of being adjacent to hemispherical taleolae, but no hemispherical taleolae have been observed in association with these.

The microstructure of the denticular plate is unique. The denticular plate has been described as being pseudopunctate for convenience only. The ventral region of the denticular plate is composed of exceedingly turbulent lamellar tissue. Toward the dorsal surface of the plate, the curled lamellae gradually become marshalled into parallel, discontinuous isoclinal folds. The crests of the isoclinal folds form the parallel ridges (semidenticles) of the dorsal surface of the plate. The axial planes of the isoclinal folds are oriented perpendicular to the hinge line and interarea, not parallel to the margin of the delthyrium. Because the isoclinal folds are oblique to the denticular plate, they crop out along the medial face of the denticular plate where they produce ridges. The axial region of each fold tends to be granular tissue without distinct boundaries. If these granular axes may be called taleolae, they are taleolae with a tabular shape. The folds and tabular taleolae are visible only in transverse and longitudinal sections. Sagittal sections are parallel to the axial planes of the folds with the result that the denticular plate is difficult to distinguish in sagittal section.

The function of pseudopuncta and taleolae is unknown. Williams (1956, p. 252) postulated that they were the "seat of attachment for tendons (tonofibrils) permeating the connective tissue of the mantle". If this be the case, it is difficult to understand why taleolae and pseudopuncta do not penetrate the secondary tissue of the shell. It would seem reasonable to assume that the visceral mass of the brachiopod animal would have been as securely fixed to the shell as the mantle. Williams suggested, also, that they had the function of pegs which riveted together the fissile lamellae of the shell. It might be suggested that taleolae are "pearls" caused by inclusion of exotic grains under the margin of the mantle or in the mantle groove. This idea is unacceptable because there are no foreign grains at the base of the taleolae, pseudopuncta may occur in a regular pattern in the shell material and the size of taleolae tends to be uniform within a species.

There tends to be a regular variation of size and distributional density of taleolae within a strophomenacean valve. Taleolae are more closely packed toward the center of the valves than toward the lateral or anterior margins of the valves. The packing is especially close in the regions of the dorsal ridges and under muscle scar areas and especially open in the muscle bounding ridges and marginal diaphragm. Text-figure 31 shows the number of taleolae per square millimeter in different regions of the disc of the valves of *Rafinesquina ponderosa* Ulrich and *Leptaena richmondensis* Foerste. Taleolae and pseudopuncta were counted on external surfaces of etched valves. The taleolae of the etched, external surfaces do not reflect variations of packing associated with internal structures. There does not seem to be an important difference in the packing density of taleolae in the exterior tissue of ventral valves compared to dorsal valves in *Rafinesquina ponderosa* Ulrich and *Leptaena richmondensis* Foerste.

The diameter of taleolae in a specimen is inversely related to the density of packing of the taleolae. Taleolae are thicker in regions of the shell where they are widely spaced than in regions where they are crowded together.

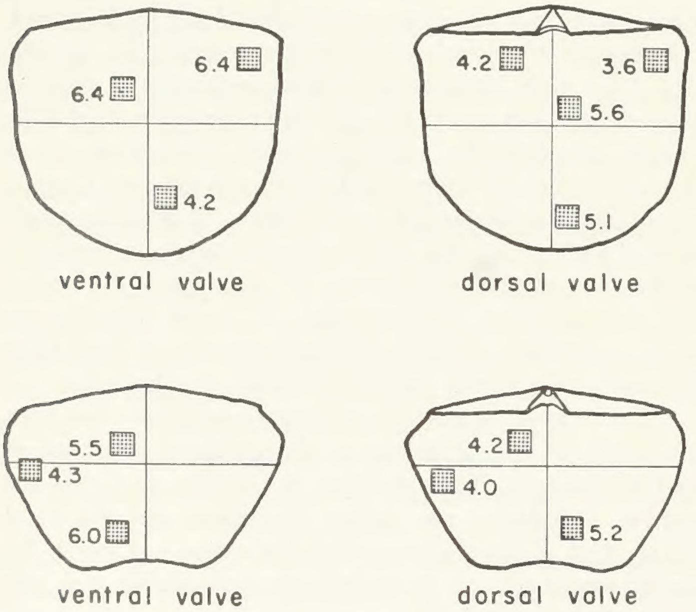
The relative size of taleolae, the density of their packing, and their pattern of occurrence in shell material may be familial differentia. These characters of the taleolae are not useful differentia because other morphological features are more evident, detailed analysis of taleolae requires destruction of the shell, and characters of the taleolae are difficult to determine in silicified and recrystallized specimens and molds. Specimens assigned to some strophomenacean genera are very rare and should not be destroyed. For example, *Hesperinia kirki* Cooper, monospecific, is represented by eight specimens; *Kirkina millardensis* Salmon, monospecific, ten specimens; *Colaptomena leptostrophoidea* Cooper, monospecific, nine specimens; *Pionomena,* three species; total of 24 specimens. *Teratelasma neumani* Cooper, monospecific, is known only from molds. All available specimens of the type species of *Kjerulfina K. trigonalis* Bancroft, of the type species of *Kjaerina, K. typa* Bancroft, and of the type species of *Hedstroemina, H. fragilis* Bancroft are molds in siltstone. Most of the known specimens assigned to *Murinella, Platymena,* and *Glyptomena* are silicified.

The number of taleolae per square millimeter has been computed for several species to demonstrate the range of packing densities. Table 4 shows the species analyzed, the number of taleolae per square millimeter and the total surface area of the shell on which the count was made. All counts were made on an etched, external surface near the center of the ventral valve.

The diameter of taleolae is variable, also, among species of strophomenaceans. Table 4 shows the mean diameter of taleolae in several species. All taleolae were measured on longitudinal peel sections from near the center of ventral valves. Measurements were made of the minimum diameter of the taleolae because taleolae may be circular, ovoid, irregularly ovoid or angular in cross-sectional shape. Moreover, the planes of the longitudinal sections are not perpendicular to all of the taleolae which were measured. The minimum diameter corresponds to the minor axis of the ellipse formed by intersection of a cylinder and an oblique plane, which is the diameter of the cylinder. Consequently, the minimum diameter is the best approximation of the true diameter of the taleolae. The measurements and the statistics derived from them are approximate because the boundaries of the taleolae are diffuse and the diameter of taleolae is known to be variable along their length.

Table 4 shows that the diameter of taleolae may vary by a factor of ×5 from species to species. The species of Table 4 are arranged in order of increasing packing density of taleolae. Inspection of the "$\bar{x}$" column shows that the mean diameter of taleolae tends to decrease as packing density increases. Column "V", coefficient of variation, shows that the standard deviation of taleolae diameters relative to mean diameters for all seven species is about the same. *Holtedahlina sulcata* (Verneuil) has the largest coefficient of variation. There seems to be no regular pattern in the position of unusually small taleolae and unusually large taleolae within this species.

*Rafinesquina ponderosa* Ulrich and *Leptaena richmondensis* Foerste also show large coefficients of variation of the size of taleolae. In addition, the taleolae of these two species tend to be arranged according to their size into patterns in the shell. The patterns may be observed both in longitudinal peels taken from the external surface of valves and in valves themselves that have been slightly etched in weak acid. The thicker taleolae of *R. ponderosa* Ulrich tend to be aligned along the deeper striae between primary costellae imparting to them an obvious radial arrangement. Large taleolae in this species, moreover, tend most commonly to occur at the intersections of these striae and prominent varices. The concentric alignment thus produced is not as apparent as the radial alignment. Smaller taleolae occur at random positions between the rows of larger taleolae. The thicker taleolae of *L. richmondensis* Foerste tend to be concentrated in concentric rows along or slightly posterior to the crests of the rugae on the disk of the valve. These taleolae also tend to occur in radial rows in the striae between costellae. These radial rows of taleolae continue across the trail of the valve where their organization into concentric rows is lacking. Small taleolae are set at random between the larger taleolae. In both species, the long axis of the oval cross section of taleolae is parallel to the costellae.



*Text-figure 31.*—The number of taleolae per square millimeter in different regions of the valves of *Rafinesquina ponderosa* Ulrich (above) and *Leptaena richmondensis* Foerste (below). The stippled squares show the areas where taleolae were counted.

Table 4. — Measurements of the packing density and diameter of taleolae

| | Packing density of taleolae | | | Diameter of taleolae | | |
|---|---|---|---|---|---|---|
| Species | #/sq. mm. | area counted in sq. mm. | N | $\bar{x}$ | s | V |
| *Megamyonia unicostata* | 4.9 | 11.1 | 20 | .052 | .0152 | 29.3 |
| *Leptaena richmondensis* | 5.5 | 11.1 | 20 | .044 | .0146 | 33.1 |
| *Rafinesquina ponderosa* | 6.4 | 11.1 | 18 | .051 | .0192 | 38.0 |
| *Tetraphalerella neglecta* | 34.0 | 11.1 | 21 | .038 | .0084 | 22.0 |
| *Oepikina minnesotensis* | 43.0 | 1.34 | 17 | .011 | .0026 | 23.1 |
| *Holtedahlina sulcata* | 78.5 | 0.67 | 20 | .011 | .0046 | 41.5 |
| *Strophomena planumbona* | 94.0 | 0.67 | 15 | .019 | .0046 | 23.9 |

N = number of taleolae measured

x = value of any measurement

$\bar{x}$ = the mean diameter of taleolae in mm. $= \frac{\Sigma\ (x)}{N}$

d = the difference between a measurement and the mean, $(x - \bar{x})$ or $(\bar{x} - x)$

s = standard deviation of taleolae diameters $= \left(\frac{\Sigma\ (d^2)}{N - 1}\right)^{1/2}$

V = coefficient of variation $= \frac{100s}{\bar{x}}$

## HABITAT AND HABITUS

Ordovician strophomenacean brachiopods are best known from rocks of marine neritic origin of North America, northern Europe, and European Russia. Species from the Southern Hemisphere, eastern Asia, southern Europe, western North America, and northern North America are poorly known. Representatives of the entire superfamily are not restricted to any specific lithotope but generally are absent from black shales and littoral sandstones. Species may show environmental selectivity by accompanying recurrent faunas.

Variation of size and thickness of Ordovician species does not support or contradict Flower's (1942, 1946, 1957) and Spjeldnaes' (1957) delineation of Ordovician climatic zones. There is a general evolutionary tendency for increase of size and thickness in all generic lineages through Ordovician time which masks potential provincial differences. Apparent correlation of size and thickness of species and geographic province is related to the age of faunas known from each province.

Strophomenacean brachiopods were part of the Ordovician benthonic fauna. Contrary to Sardeson (1929), probably no species led a planktonic existence. Ephebic individuals of most leptaenid species and older oepikinid and strophomenid species probably were attached to the substrate by a thin pedicle. At least, adults of these groups have an open pedicle foramen. Ephebic individuals of all other species have a plugged pedicle conduit from which may be inferred a functional pedicle and a tethered existence during nepionic development.

A problem which has never been successfully resolved concerns the preferred orientation of strophomenaceans during life. They may have stood upon the cardinal margin, hung pendent from floating objects, or they may have been recumbent upon the sea-floor. Sardeson (1929) suggested that species of *Strophomena* and resupinate allies hung pendent from floating objects and that species of *Oepikina* cemented themselves in an upright position to the substrate. Sardeson's conclusions were based upon the attitude of specimens within a bentonitic stratum. There is no structure of the resupinate group which could be concerned with suspension, as, for example, the spines of chonetoids and linoproductids. Moreover, if individuals lived suspended, it is difficult to explain restriction of species to (and from) specific lithologies. It is most unlikely that concavo-convex forms, such as *Oepikina,* lived in an erect position. The umbo of concavo-convex species is not deformed to indicate cementation as found among orthotetids. Uncemented to the substrate, a flattened concavo-convex individual could not stand upon its narrow cardinal margin in the slightest water current unless many individuals were imbricated together, as in the shingling of *Rafinesquina fracta* (Meek) in the Fairmount Formation of Cincinnati, Ohio. In reality, the shingling of *Rafinesquina* is probably a thanatocoenosic condition inasmuch as the imbricated valves generally occur in current-scoured channels.

It is assumed generally that strophomenaceans rested upon the convex valve to elevate the anterior commissure away from the muddy substrate. Undoubtedly, untethered strophomenaceans lived in any position in which they could perform all of their body functions. Evidence tends to indicate that unattached strophomenaceans rested upon the concave or planate valve. The evidence is circumstantial and subject to contradition. Nevertheless, the following observations support this hypothesis.

It is unusual to find the thin outer carbonate layer preserved on the surface of strophomenaceans. The outer carbonate layer is usually abraded from the surface except where it is preserved under incrustations. The rare occurrences of unprotected outer carbonate layer are most commonly found near the margin of the concave valve. The occurrence is marginal because the margin is the last-formed part of the valves and had the least time of abrasion before burial. The valve upon which the brachiopod rested was subjected to less abrasion than the overlying valve.

Two specimens of the ventral valve of *Rafinesquina* cf. *ponderosa* in the collections of the University of Cincinnati bear massive, discoidal bryozoan zoaria on the external surface. The bounding ridges around the diductor muscle scars, the radial ridges of the diductor muscle scars, and the medial ridges of each valve are enlarged grotesquely. The diductor muscles must have lifted the bryozoan colony as well as the ventral valve when the valves were opened.

The suggested life-position negates the problem of hydrodynamic instability, discussed by Menard and Boucot (1951), that would have been present if the convex valve were downward during life. Also, it is most common to find the exterior of convex valves exposed on the upper surface of strata and the exterior of concave or planate valves exposed on the underside of strata. It has been argued that the attiude of valves in strata is caused by *post mortem* turning of valves by water currents. Untethered species probably had little control of their attitude during life and would also have been subject to turning by water currents.

It is more common to find argillitic matrix than sparry calcite in contact with the inner surface of the concave valve in thin sections. The sparry calcite probably represents post-depositional filling of gas pockets within the valves.

A census has been made of epizoic organisms on valves of species of *Rafinesquina* from two lenses in the Waynesville Formation of Butler County, Ohio, and Franklin County, Indiana. Only clean, articulated specimens were selected for the census. Of the 358 specimens considered, 28% have epizoic organisms on the convex valve only, 13% have epizoic organisms on the concave valve only, 30% have no epizoic organisms, 9% have epizoic organisms equally developed on both valves, 14% have larger epizoic incrustations on the convex valve than on the concave valve, and 6% have larger epizoic incrustations on the concave valve than on the convex valve. Sixteen individuals have fossil fragments piercing the concave valve or incorporated into the concave valve during growth. Only two individuals show fossil fragments which project into the ventral valve. The epizoic organisms which were noted include Bryozoa, inarticulate brachiopods, crinoid bases, dendroid bases, and annelid tubes.

Hyman (1958, p. 585) stated that modern brachiopods, except lingulids, usually take a horizontal position, with the larger ventral valve uppermost "but may erect to a vertical position by manipulating the adjustor muscles of the pedicle". Tethered shells would naturally rest upon the concave valve because of current action.

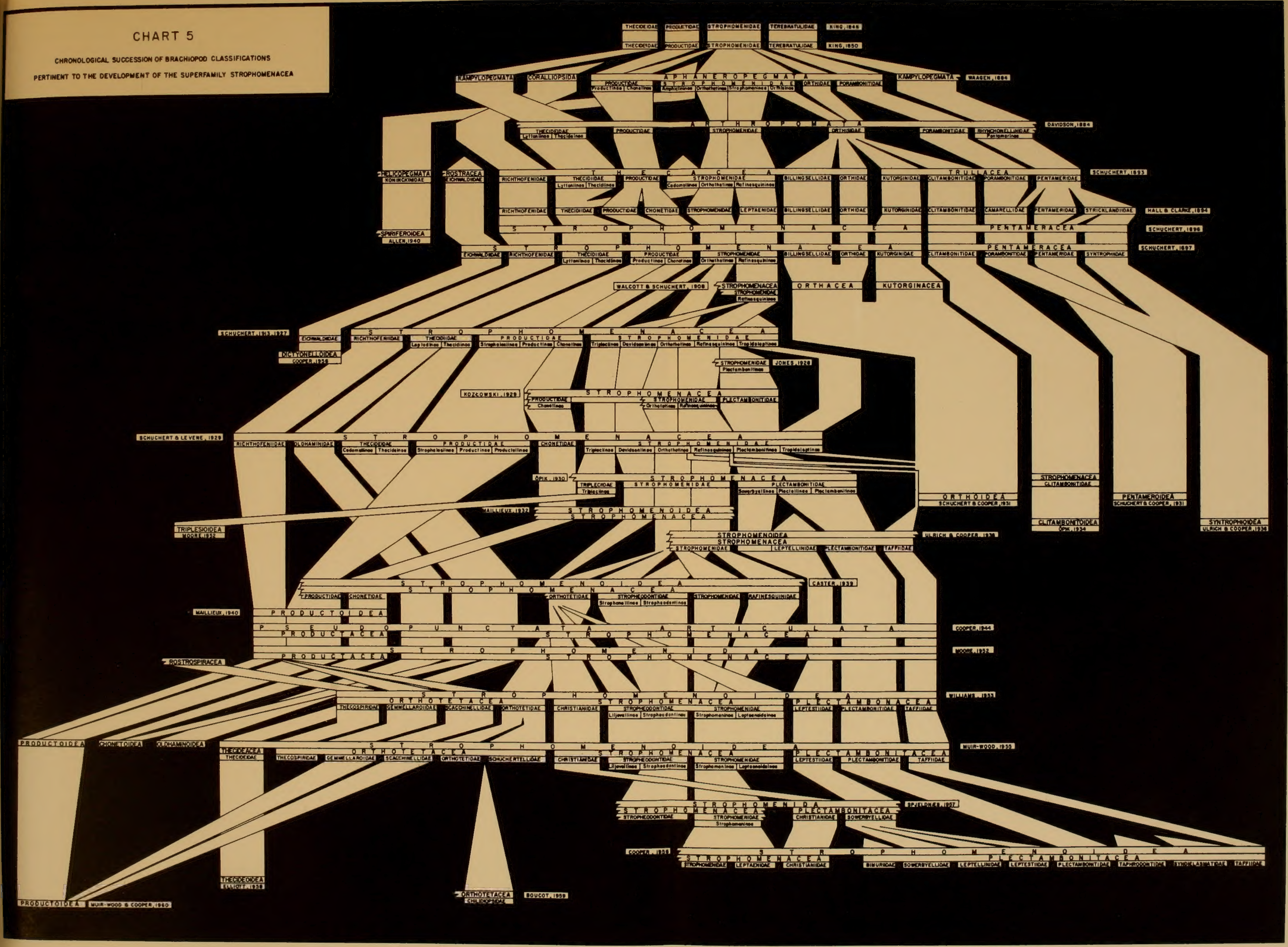
Consideration of water circulation within strophomenaceans conflicts with this hypothesis. Water circulation is assumed to have been in the same direction as occurs among living articulates, *i.e.* incurrent areas lateral, excurrent areas antero-medial. Authors have presumed that the commissure was elevated to avoid suffocation, that is, that the living animal rested upon the convex valve. Possibly the curling of the ceradinal angles in the direction of the convex valve, ventrally in *Oepikina* and dorsally in *Strophomena* and *Tetraphalerella,* served for ingress of water from above the sediment interface at the posterior-lateral corner of the valves. The marginal diaphragm, which is well developed in *Murinella, Oepikina, Leptaena, Cyphomena,* and *Strophomena* may have restricted ingress of sediment when the valves were parted and may have directed the flow of water within the animal. A posterior-lateral depression in the marginal diaphragm, which is observed in many species, may be the site of water ingress. The biconvex, folded species of the Furcitellini, including *Holtedahlina sulcata* (Verneuil), commonly lack a marginal diaphragm. Possibly folding of the valves permitted ingress of water without the necessity of a sediment barrier or a channel way to conduct water into the mantle cavity.

There are no published measurements of the possible anterior gape of strophomenacean brachiopods. Sagittal sections show that the valves might have opened until the ventral edge of the chilidium came into contact with the dorsal edge of the pseudodeltidium, as shown in Text-figure 24, section A. Sagittal sections through the chilidium and pseudodeltidium do not show the axis of rotation of the valves, but sagittal sections lateral to the teeth do show the axis of rotation of the valves. Text-figure 24, section D. An enlarged outline of a lateral sagittal section of *Strophomena planumbona* (Hall) was accurately positioned upon an outline of an exact medial sagittal section of the same specimen. Graphic analysis shows that one valve was capable of 5° of rotation with respect to the other valve. The specimen studied was neither unusually large or small. It was 20.5 mm long from the axis of rotation to the antero-central commissure along a straight line. The individual was capable of a maximum of 2 mm gape at the anterior margin. If thick diductor muscles overlay the ventral ends of the cardinal process lobes, or if a periostracal pad existed along the hinge line, the actual possible gape may have been less than 2 mm.

In addition to the epizoic organisms mentioned, strophomenaceans were subject to parasitism by boring sponges and predation by gastropods. Fragments of both *Rafinesquina* and *Strophomena* that were drilled presumably by gastropods, of unestablished species, have been found in Richmondian rocks. No earlier examples are known. Many species of strophomenaceans from throughout the Ordovician show predation by creatures which attacked the margin of the mantle and shell. Attack upon the mantle margin produced deformation of later costellae and varices without discontinuity of these features. Many specimens show evidence that pieces of the shell margin were broken or bitten-off during ontogeny. These accidents or depredations produced great deformation of the shell and discontinuity of the prosopon. Evidence of removal of pieces of shell is more common on convex valves than on concave valves. *Rafinesquina winchesterensis* Foerste from a lens in the Cynthiana Formation, Carntown, Kentucky, and *R. ponderosa* from a lens in the Waynesville Formation, along Indian Creek, Butler County, Ohio, show a high frequency of breakage or predation by removal of shell pieces during mid-life of the individuals. The predator, if such it was, probably invaded the shellbank, attacked many brachiopods, and left.

## CHART 5

CHRONOLOGICAL SUCCESSION OF BRACHIOPOD CLASSIFICATIONS PERTINENT TO THE DEVELOPMENT OF THE SUPERFAMILY STROPHOMENACEA



THECIDEIDAE PRODUCTIDAE STROPHOMENIDAE TEREBRATULIDAE KING, 1846
THECIDEIDAE PRODUCTIDAE STROPHOMENIDAE TEREBRATULIDAE KING, 1850
KAMPYLOPEGMATA CORALLIOPSIDA APHANEROPEGMATA PRODUCTIDAE Productinae Chonetinae STROPHOMENIDAE Amphiclininae Orthothetinae Strophomeninae Orthisinae ORTHIDAE PORAMBONITIDAE KAMPYLOPEGMATA WAAGEN, 1884
ARTHROPOMATA THECIDEIDAE Lyttoniinae Thecideinae PRODUCTIDAE STROPHOMENIDAE ORTHISIDAE PORAMBONITIDAE RHYNCHONELLIDAE Pentamerinae DAVIDSON, 1884
HELICOPEGMATA KONINCKINIDAE ROSTRACEA EICHWALDIIDAE THECACEA RICHTHOFENIIDAE THECIDIIDAE Lyttoniinae Thecidiinae PRODUCTIDAE STROPHOMENIDAE Cadomellinae Orthothetinae Rafinesquininae BILLINGSELLIDAE ORTHIDAE KUTORGINIDAE TRULLACEA CLITAMBONITIDAE PORAMBONITIDAE PENTAMERIDAE SCHUCHERT, 1893
RICHTHOFENIIDAE THECIDIIDAE PRODUCTIDAE CHONETIDAE STROPHOMENIDAE LEPTAENIDAE BILLINGSELLIDAE ORTHIDAE KUTORGINIDAE CLITAMBONITIDAE CAMARELLIDAE PENTAMERIDAE STRICKLANDIIDAE HALL & CLARKE, 1894
STROPHOMENACEA PENTAMERACEA SCHUCHERT, 1896
SPIRIFEROIDEA ALLEN, 1940
STROPHOMENACEA EICHWALDIIDAE RICHTHOFENIIDAE THECIDIIDAE Lyttoniinae Thecidiinae PRODUCTIDAE Productinae Chonetinae STROPHOMENIDAE Orthothetinae Rafinesquininae BILLINGSELLIDAE ORTHIDAE KUTORGINIDAE PENTAMERACEA CLITAMBONITIDAE PORAMBONITIDAE PENTAMERIDAE SYNTROPHIIDAE SCHUCHERT, 1897
WALCOTT & SCHUCHERT, 1908 STROPHOMENACEA STROPHOMENIDAE Rafinesquininae ORTHACEA KUTORGINACEA
SCHUCHERT, 1913, 1927 STROPHOMENACEA EICHWALDIIDAE RICHTHOFENIIDAE THECIDIIDAE Lyttoniinae Thecidiinae PRODUCTIDAE Strophalosiinae Productinae Chonetinae STROPHOMENIDAE Triplesiinae Davidsoniinae Orthothetinae Rafinesquininae Tropidoleptinae
DICTYONELLOIDEA COOPER, 1956
STROPHOMENIDAE Plectambonitinae JONES, 1928
KOZŁOWSKI, 1929 STROPHOMENACEA PRODUCTIDAE Chonetinae STROPHOMENIDAE Orthotetinae Rafinesquininae PLECTAMBONITIDAE
SCHUCHERT & LEVENE, 1929 STROPHOMENACEA RICHTHOFENIIDAE OLDHAMINIDAE PRODUCTIDAE Cadomellinae Thecidiinae Strophalosiinae Productinae Productellinae CHONETIDAE STROPHOMENIDAE Triplesiinae Davidsoniinae Orthothetinae Rafinesquininae Plectambonitinae Tropidoleptinae
ÖPIK, 1930 STROPHOMENACEA TRIPLECIIDAE Triplesiinae STROPHOMENIDAE PLECTAMBONITIDAE Sowerbyellinae Plectellinae Plectambonitinae
STROPHOMENACEA CLITAMBONITIDAE ORTHOIDEA SCHUCHERT & COOPER, 1931 PENTAMEROIDEA SCHUCHERT & COOPER, 1931
MAILLIEUX, 1932 STROPHOMENOIDEA STROPHOMENACEA
TRIPLESIOIDEA MOORE, 1952
CLITAMBONITOIDEA ÖPIK, 1934 SYNTROPHIOIDEA ULRICH & COOPER, 1936
STROPHOMENOIDEA STROPHOMENACEA STROPHOMENIDAE LEPTELLINIDAE PLECTAMBONITIDAE TAFFIIDAE ULRICH & COOPER, 1936
STROPHOMENOIDEA STROPHOMENACEA PRODUCTIDAE CHONETIDAE ORTHOTETIDAE STROPHEODONTIDAE Stropheodontinae Strophonellinae STROPHOMENIDAE RAFINESQUINIDAE CASTER, 1939
MAILLIEUX, 1940 PRODUCTOIDEA
PSEUDOPUNCTATA ARTICULATA PRODUCTACEA STROPHOMENACEA COOPER, 1944
STROPHOMENIDA PRODUCTACEA STROPHOMENACEA MOORE, 1952
ROSTROSPIRACEA
STROPHOMENOIDEA ORTHOTETACEA STROPHOMENACEA PLECTAMBONACEA THECOSPIRIDAE GEMMELLAROIIDAE SCACCHINELLIDAE ORTHOTETIDAE CHRISTIANIIDAE STROPHEODONTIDAE Lilljevallinae Stropheodontinae STROPHOMENIDAE Strophomeninae Leptaenoideinae LEPTESTIIDAE PLECTAMBONITIDAE TAFFIIDAE WILLIAMS, 1953
PRODUCTOIDEA CHONETOIDEA OLDHAMINOIDEA
THECIDEACEA THECIDEIDAE STROPHOMENOIDEA ORTHOTETACEA THECOSPIRIDAE GEMMELLAROIIDAE SCACCHINELLIDAE ORTHOTETIDAE SCHUCHERTELLIDAE STROPHOMENACEA CHRISTIANIIDAE STROPHEODONTIDAE Lilljevallinae Stropheodontinae STROPHOMENIDAE Strophomeninae Leptaenoideinae PLECTAMBONITACEA LEPTESTIIDAE PLECTAMBONITIDAE TAFFIIDAE MUIR-WOOD, 1955
STROPHOMENIDA STROPHOMENACEA STROPHEODONTIDAE STROPHOMENIDAE Strophomeninae PLECTAMBONITACEA CHRISTIANIIDAE SOWERBYELLIDAE SPJELDNAES, 1957
COOPER, 1956 STROPHOMENOIDEA STROPHOMENACEA STROPHOMENIDAE LEPTAENIDAE CHRISTIANIIDAE PLECTAMBONITACEA BIMURIDAE SOWERBYELLIDAE LEPTELLINIDAE LEPTESTIIDAE PLECTAMBONITIDAE TAPHRODONTIDAE SYNDIELASMATIDAE TAFFIIDAE
THECIDEOIDEA ELLIOTT, 1958
ORTHOTETACEA CHILIDIOPSIDAE BOUCOT, 1959
PRODUCTOIDEA MUIR-WOOD & COOPER, 1960

Orthoconic nautiloid cephalopods are common in both localities. No evidence can be offered for predation by trilobites, as suggested by Sardeson (1929). Their manducatory apparatus would appear to have been quite unsuited to such habits.

The interior of strophomenoid specimens that have sectioned for study are commonly packed with ovoid, argillitic pellets. The pellets are probably coprolites of scavenging organisms.

No information has been found concerning the nutrition, excretion or reproduction of strophomenacean brachiopods. Evidence of sexual dimorphism has not been found. There is no evidence to suggest that the untethered strophomenaceans could move in the manner of pectens.

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## EVOLUTION AND CLASSIFICATION OF THE LUCINIDAE (MOLLUSCA; BIVALVIA)

By

SARA S. BRETSKY

1976

Paleontological Research Institution
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(Founded 1917)

VOL. VIII

No. 50

A Lewis G. Weeks Publication

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Sara S. Bretsky

October 8, 1976

Paleontological Research Institution
Ithaca, New York, U.S.A. 14850

*Library of Congress Card Number: 76-40886*

Printed in the United States of America
Arnold Printing Corporation
Ithaca, N.Y.

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# EVOLUTION AND CLASSIFICATION OF THE LUCINIDAE (MOLLUSCA; BIVALVIA)

Sara S. Bretsky

## ABSTRACT

This paper summarizes the evolution of the family Lucinidae (Mollusca; Bivalvia) and proposes a new classification of the family. Evidence is presented indicating that the lucinoids are the ancestral stock of the subclass Heterodonta. The classification used herein divides the Lucinidae into seven genera — *Lucina, Codakia, Miltha, Myrtea, Anodontia, Loripes,* and *Divaricella,* the first five of which are regarded as monophyletic lineages. The section on systematics redescribes 42 North American and European Tertiary and Recent species, representing 28 subgenera; most of the species redescribed are the type species of the respective subgenera.

## INTRODUCTION

In two earlier papers (Bretsky, 1970, 1971), I have presented an evaluation of the efficacy of numerical taxonomy (*sensu* Sokal and Sneath, 1963) by comparing an original phylogenetic classification of certain species of the family Lucinidae (Mollusca; Bivalvia) to phenetic classifications of these species. The reader of these papers has had to take the validity of the phylogenetic classification on faith; this paper presents a detailed documentation of that classification and the evolutionary hypotheses from which it is derived. The classification of the Lucinidae here presented was mostly formulated before the publication of that of Chavan (1969) in the *Treatise on Invertebrate Paleontology,* and it differs from Chavan's scheme in several respects.

Allen (1958) showed that the Lucinidae and their relatives, the Thyasiridae and Ungulinidae, differ from most of the presumably evolutionarily advanced eulamellibranch heterodonts, with which the lucinoids have usually been classified, in possessing an anterior inhalant feeding current, an unusually elongated anterior adductor whose cilia sort food particles, and associated deviations of the gills and digestive tract from the typical eulamellibranch pattern seen in such familiar clams as *Mercenaria* and *Mya.* [See R. C. Moore, ed. (1969) for an outline of the morphology and classification of the Bivalvia.] Allen interpreted these features as secondary specializations to inhospitable marginal environments; McAlester (1964, 1965, 1966) pointed out that forms probably ancestral to the Lucinidae are present in Middle Ordovician strata, and reasoned that the anterior inhalant current and associated anatomical features are actually evidence of the primitiveness of the taxon. Following McAlester, Stanley (1968), in his study of the adaptive radiations of the Bivalvia, considered the lucinoids an evolutionarily separate group which had not given rise to other important eulamellibranch taxa. Boss (1969), however, demonstrated that in most anatomical features not related to feeding, the Lucinacea are similar to other eulamellibranch superfamilies. Allen (1968) described a Recent crassatelloid species — the Crassatellacea (= Astartacea) are generally regarded as the stem stock of the Eulamellibranchia (Stanley, 1968) — which has an anterior inhalant current and associated features of the feeding apparatus which correspond to those of the lucinoids. Jackson (1970, 1973) showed that the dominance of the Lucinacea in marginal environments is not a matter of competitive exclusion by more advanced forms, but an adaptation to a rich food supply made up of large particulate material not exploitable by conventional eulamellibranchs, with their sievelike gills which reject large particles. On the basis of these findings, it is here postulated that early Paleozoic lucinoids were ancestral to all other eulamellibranch taxa — a phylogenetic hypothesis which accords with their formal classification as the first group of the subclass Heterodonta in the *Treatise on Invertebrate Paleontology.*

This paper deals in detail with the systematics of 42 Tertiary and Recent lucinid species, which were used as operational taxonomic units (Sokal and Sneath, 1963) in the phenetic classifications referred to above. Of these species, 39 are from North America and the rest from Europe. The constraints on the choice of species for study were as follows: I used taxa which generally were represented by a fairly large number of individuals in the collections of four major museums (the Peabody Museum of Natural History, Yale University, New Haven, Connecticut; National Museum of Natural History [U. S. National Museum], Washington, D. C.; the Academy of Natural Sciences of Philadelphia, Pennsylvania; and the Paleontological Research Institution, Ithaca, New York); these museums house most of the type material of lucinid species which have been described by North American systematists. Because of the necessity of recording a large number of characters for the numerical taxonomic study, I included only fossil species which were well enough preserved that the number of characters obtainable was closely comparable with the number scored for the Recent species (only shell data were used, since information on the soft parts was unobtainable for many of the Recent species). Because most numerical taxonomic studies dealt only with species considered to belong to the same genus or to a few closely related genera, I was interested in exploring the degree of correspondence between phenetic and phylogenetic relationships at higher hierarchic levels. Vokes (1966) had just completed a compilation of names of all known genus-group bivalve taxa, and I used all the taxa included in this compilation for which there was available material fitting these criteria of preservation. I preferentially used type species of the various genera as most objectively reflecting the original describer's concept of the taxon. To provide broad taxonomic coverage while still dealing with a manageable number of species, in most instances I used only one species from each genus-group taxon (of which 29 were represented in the study). In some cases I used two, three, or four species considered by earlier workers (particularly Dall, 1901b, and Chavan, 1937, 1938) to belong to a single genus-group taxon.

Although this paper presents detailed descriptions of only the 42 species used in the numerical taxonomic study, during the course of this investigation I looked at specimens of about 200 other lucinid species and at descriptions and illustrations of perhaps 500 more. In the discussions of the distribution and phylogenetic relationships of the subgenera treated herein, I have indicated the probable affinities of those additional species of which I have seen specimens, as well as of some which I know only from the literature but which are important to the interpretation of the affinities of the species and subgenera discussed in detail. The phylogenetic classification and discussion of the course of lucinid evolution presented below is a distillation of the more detailed section on systematics.

## ACKNOWLEDGMENTS

An earlier version of this paper was submitted to Yale University in 1969 as a Ph. D. dissertation. Financial support was provided by a National Science Foundation Graduate Fellowship. Funds for travel were provided by the Department of Geology and Geophysics, Yale University; and a grant from the Society of the Sigma Xi defrayed the expenses of photography.

For suggesting the original project and for his constant interest and encouragement throughout the study, I am particularly indebted to A. Lee McAlester, formerly of Yale University. I also thank Karl M. Waage, Donald C. Rhoads, and Willard D. Hartman of Yale University; Kenneth J. Boss of the Museum of Comparative Zoology, Harvard University; and Peter W. Bretsky of the State University of New York at Stony Brook for reading and commenting on various drafts of the manuscript.

For providing access to collections of lucinid specimens, I thank Willard Hartman and Copeland MacClintock of Yale University; Erle G. Kauffman and Joseph Rosewater of the U.S. National Museum; R. Tucker Abbott (formerly) and Horace G. Richards of the Academy of Natural Sciences of Philadelphia; and Katherine V. W. Palmer of the Paleontological Research Institution. I also thank Arthur L. Howland and Laurence L. Sloss of Northwestern University and Rainer Zangerl of the Field Museum of Natural History for making available office and laboratory space from 1967 through 1970.

I have profited greatly from discussions of questions of lucinid ecology and systematics with Erle Kauffman and his students, Robert Vostreys and Robert Beauchamp; with Joseph C. Britton of Texas Christian University; and with Jeffrey S. Levinton of the State University of New York at Stony Brook. I owe a special debt to Jeremy B. C. Jackson of Johns Hopkins University for access to his study of the ecology of Recent Lucinidae before its publication.

For invaluable help in preparing the manuscript, I thank Miss Pauline Mohr, who drafted the phylogenetic diagrams; Miss Osa Kendrick, who did much of the photographic work; and Miss Linnea Danchi and Miss Nancy Millea, who typed various versions of the text.

Funds for publication of this paper have been furnished by National Science Foundation Grant GB-27441.

## MORPHOLOGY, ECOLOGY, EVOLUTIONARY SIGNIFICANCE, AND CLASSIFICATION OF THE LUCINIDAE

An understanding of the evolution and classification of the Lucinidae requires a consideration of the relationship between this family and other major taxa of the Bivalvia. In the most recent classification of the bivalves, the Bivalvia volume of the *Treatise on Invertebrate Paleontology* (R. C. Moore, ed., 1969), the Lucinidae are placed in the superfamily Lucinacea, which also includes the families Thyasiridae, Mactromyidae, Fimbriidae, Ungulinidae, and Cyrenoididae. [Subsequent work by Allen and Turner (1970) and Boss (1970) has shown that Recent representatives of the Fimbriidae are anatomically closely similar to species of the Lucinidae; Boss retained the name Fimbriidae, but Allen and Turner considered it unnecessary.] Following the suggestion of McAlester (1966), the genus *Babinka,* which McAlester (1964, 1965, 1966) considered ancestral to the taxa placed in the Lucinacea, is referred to the family Babinkidae and superfamily Babinkacea. A detailed study by Allen (1958) of the Lucinidae, Thyasiridae, and Ungulinidae [= Diplodontidae] emphasized the close relationship between these families and their unique divergences from the anatomical groundplan of such "typical" bivalves as the venerids or the myids.

## ANATOMY AND ECOLOGY OF THE LUCINACEA

Most early classifications of the Bivalvia were essentially monothetic (*sensu* Sneath, 1962), being based wholly or primarily on either the characters of the hinge or the structure of the gills. By both criteria the Lucinacea were considered evolutionarily advanced, their dentition being heterodont and their gills eulamellibranch [see Cox (1969) for definitions, discussions, and illustrations of the terminology applied to the hard and soft parts of bivalves].

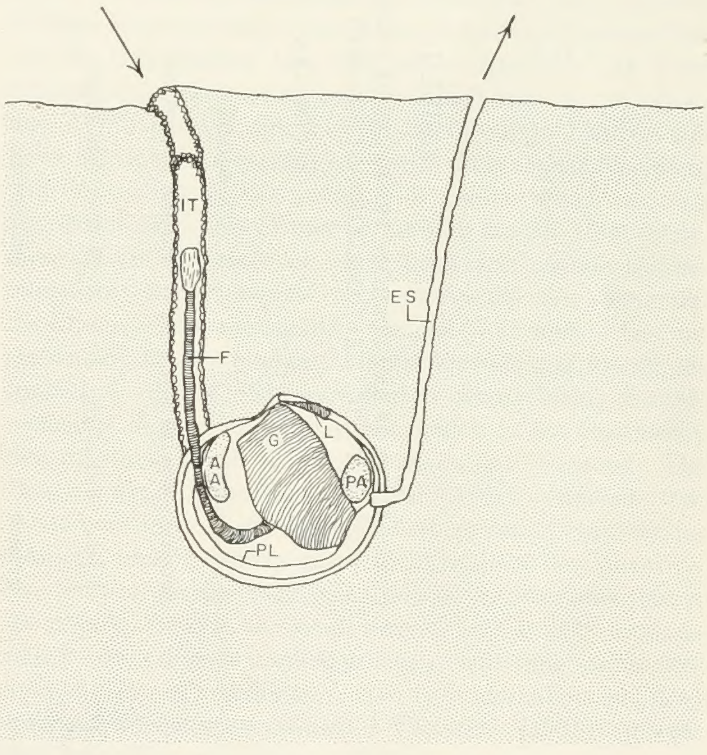
The Lucinacea are infaunal and are apparently suspension feeders, like most other eulamellibranchs. But the major feeding current in the Lucinacea is anterior (as in the protobranch *Nucula*), not posterior (as in most eulamellibranchs). The anterior current is not channeled by siphons; instead, the Lucinacea have a long, vermiform foot which can be extended to several times the length of the shell (Text-fig. 1; Table 1), and which, in addition to its normal burrowing function, is used to construct a feeding tube. Glands in the tip of the foot secrete mucus which cements substratum particles together. The tube extends vertically upward from the anterior end of the shell, the last two or three millimeters of it turning horizontally along the surface of the substratum (Text-fig. 1).

In most infaunal bivalves the anterior and posterior adductor muscles are subequal in size. In the Lucinacea, however, the anterior adductor is considerably longer than the posterior one. It is divided into a round or oval dorsal "catch" portion and elongate ventral "quick" portion (Text-fig. 1; Allen, 1958, fig. 1a-c). The elongate adductor forms a shelf in front of the mouth. The epithelium of the anterior adductor is ciliated, and most of the sorting out of food particles brought in by the inhalant current is done by these cilia, rather than by those of the gills. In the Lucinidae and Thyasiridae, virtually all the sorting is done on the anterior adductor; however, in the Ungulinidae, whose anterior adductor is less ciliated and relatively shorter than those of the other two families, the gills play a greater role in sorting of food particles.

The eulamellibranch gill consists of a pair of lamellae (demibranchs) held together by interlamellar and interfilamentar tissue. The demibranchs may be about equal in size, or the outer one may be shorter dorsoventrally than the inner. In the Ungulinidae, the outer demibranch is about half the length of the inner one; in the Thyasiridae, the outer demibranch is about a third as long as the inner. The Lucinidae have only one demibranch. In the Thyasiridae and Lucinidae, the gill is thick and fleshy as a result of the development of a considerable amount of subfilamentar tissue, in contrast to the thin demibranchs of the Ungulinidae (Table 1). The ciliation of the gills of the Ungulinidae and Thyasiridae is comparable in complexity to that of most other eulamellibranchs, but in the Lucinidae there is practically no specialization of the cilia. Another difference between the gills of the Lucinacea and those of other eulamellibranchs is in the position of attachment of the gills; they are not parallel to the anterior-posterior axis of the body, but diagonal to it (Text-fig. 1). This tilting of the gills provides room in the mantle cavity for the foot when it is withdrawn after forming the feeding tube (Kauffman, 1967).

The palps of the Lucinidae are small and simple; those of the Thyasiridae and Ungulinidae are larger, with a number of specialized ciliary tracts. The complexity of gill and palp mechanisms in the various families is inversely proportional to the efficiency of the ciliary sorting area on the anterior adductor.

The Lucinacea have posterior inhalant and exhalant currents, but the posterior inhalant current is weak and does not play an important part in feeding. The stronger posterior exhalant current, as in other bivalves, serves for the disposal



Text-figure 1. Living position of a generalized lucinid, modified from Allen (1958) and Kauffman (1967). Left valve removed to show anatomy, and anterior inhalant tube broken away to show shape of foot. Arrows show direction of inhalant and exhalant currents.

Key to symbols: IT, inhalant tube; F, foot; AA, anterior adductor muscle; G, gill; PA, posterior adductor muscle; L, ligament; ES, exhalant siphon; PL, pallial line.

## TABLE 1

COMPARISON OF ANATOMICAL FEATURES OF THREE FAMILIES OF THE LUCINACEA AND A TYPICAL EULAMELLIBRANCH FAMILY [DATA FROM ALLEN (1958)]

| | LUCINACEA | | | TYPICAL EULAMELLIBRANCH |
|---|---|---|---|---|
| | Lucinidae | Thyasiridae | Ungulinidae | Veneridae |
| Main feeding current | anterior, through tube | anterior, through tube | anterior, through tube | posterior, through siphon |
| Maximum vertical extension of foot | 6 times shell length | 10 times shell length | 3 times shell length | not extensible |
| Relative elongation of anterior adductor | greatest | intermediate | least | not elongated |
| Major site of sorting of particles | anterior adductor | anterior adductor | gills | gills |
| Cross-sectional shape of gill | one thick demibranch | two thick demibranchs | two thin demibranchs | two thin demibranchs |
| Ciliation of gills | simple | complex | complex | complex |
| Position of gills | diagonal to anterior-posterior axis | diagonal to anterior-posterior axis | diagonal to anterior-posterior axis | parallel to anterior-posterior axis |
| Ciliation of palps | simple | intermediate | complex | complex |
| Posterior exhalant aperture | siphon which inverts into suprabranchial | simple aperture, no siphon | simple aperture, no siphon | siphon which retracts into pallial sinus |
| Rejection tracts in stomach | absent | absent | present | present |

of wastes. In the Ungulinidae and Thyasiridae, there is no exhalant siphon, but apertures are formed by fusion of the inner lobes of the mantle. The exhalant current discharges into the sediment surrounding the shell. Some members of the Lucinidae have a unique exhalant siphon. It is a long tube, formed from the inner mantle lobe, which can be extended upward to the sediment surface or downward into the sediment (Allen, 1958; Stanley, 1970), so that wastes can be discharged at some distance from the shell. The Lucinidae have no pallial sinus; rather, when the siphon is to be retracted, it is first shortened by a pair of small muscles. It then inverts and lies in the suprabranchial cavity.

A final important difference between the Lucinacea and other eulamellibranchs is in the structure of the stomach. The lucinoid stomach appears to be specialized for dealing with large food particles. The sievelike structure of the gills of those eulamellibranchs which use the gills as sorting areas, as well as their ciliated labial palps, screen out most large particles, and there are also ciliated sorting areas within the stomach which perform another cycle of rejecting large particles. In the Lucinacea, there is less rejection of large particles by the sorting mechanisms of the anterior adductor, the gills, or the palps. The stomach of the Ungulinidae has a number of ciliated sorting areas, but these are virtually absent in the Thyasiridae and Lucinidae.

Allen (1958) believed that "the Lucinacea live in environments where the food supply is so low that all available particulate food must be accepted and thus sorting mechanisms are necessarily poorly developed" (Allen, 1958, p. 480). Jackson (1970) pointed out, however, that in tropical areas where lucinoids are dominant — usually communities characterized by the presence of marine angiosperm grasses — there is an abundant supply of food particles which are too large to be utilized by conventional filter-feeding mechanisms. As Allen (1958) noted, frequently several species of lucinoids occur together in environments in which the only other important bivalves in the fauna are the deposit-feeding nuculoids. H. B. Moore, *et al.* (1968) showed that, contrary to Allen's belief that lucinoids occur only in areas lacking a rich infauna, over 4 million individuals of several lucinid and ungulinid species inhabited a tidal flat in Florida (which was mostly covered with marine grasses) about 60,000 m$^2$ in area. In this community the Lucinacea made up about 75% of the biomass and about 60% of the individuals of the molluscan infauna. They were associated with species of several other eulamellibranch superfamilies (veneroids, carditoids, and tellinoids) and with various infaunal annelids. As Allen (1958), Stanley (1970), and Jackson (1970) found, the areas in which lucinoids are dominant are frequently characterized by a high degree of ecological stress, such as large fluctuations in temperature and salinity, stagnant conditions, and the presence of hydrogen sulfide. These conditions may interact with the unusual food supply to reinforce the exclusion of stenotopic eulamellibranchs from these areas.

On the basis of Allen's conclusions about lucinoid ecology, it was assumed [*e.g.*, McAlester (1966), Kauffman (1967), Stanley (1968)] that the Lucinacea in general are competitively inferior to most "normal eulamellibranchs". Under this interpretation, however, it was difficult to account for the fact that the lucinoids not only survived but diversified during the Mesozoic invasion of the infaunal niche by the siphonate eulamellibranchs (Stanley, 1968) and that their subsequent Late Cretaceous-early Tertiary and mid-Tertiary radiations parallelled those of the other eulamellibranchs. The work of Jackson (1970, 1973) indicated that the situation is not simply a question of competitive exclusion of the Lucinacea from normal-marine habitats. Jackson studied tropical lucinids and ungulinids in shallow-water, stressful environments; he found that the Lucinidae of these areas are more tolerant to physiological stress than are the Ungulinidae, but that some ungulinids are more tolerant than most nonlucinoid eulamellibranchs are. Jackson (1973) pointed out that in general larger bivalves are more tolerant to physiological stress than are smaller ones, and that nearly all the species of Lucinidae which occur in high-stress areas are 15 mm or more in length. Conversely, these species are rare in or absent from shelf regimes characterized by more "normal" and more stable environmental conditions, where the smaller lucinids (5-15 mm in length) are usually most abundant. All the lucinids and ungulinids studied by Allen (1958) were shallow-water forms; thus his ecological data refer to a regime which is not necessarily that inhabited by all or even the majority of lucinoids. The data on depth preferences in Dall (1901b) indicate that about two-thirds of the West Indian species of lucinids, for example, inhabit normal-marine shelf regimes. Few quantitative data on marine shelf communities are available, but it seems probable that the small lucinids of the shelf are associated with a diverse molluscan fauna containing representatives of many eulamellibranch taxa [cf. the shallow and deep inner sublittoral associations of Valentine (1961) and the shelf assemblages of Parker (1964)].

Jackson (1970) generalized that within the tropical lucinoids, the Lucinidae are most common nearshore and the Ungulinidae offshore. The Thyasiridae, which usually inhabit cold waters, have not been well studied ecologically; Allen (1958) collected specimens of only one thyasirid species.

Kauffman (1967), who compiled data on Recent occurrences of thyasirids, considered this family to be characteristic of "cool waters and soft mud substrate in areas of low biotic productivity" and of associations low in faunal diversity. His data cover both shelf and deep-sea environments. His localities are all Arctic or boreal; as Dunbar (1970) pointed out, the Arctic region is characterized both by low productivity and by a "highly oscillating basic food supply . . . the oscillation being annual in period". In this environment, Dunbar stated, herbivores "must develop a degree of omnivorous habit, using detritus, microzooplankton and dissolved organic material". It is possible that the basic lucinoid adaptation to fairly indiscriminate processing of all available food is selectively advantageous under Arctic conditions as well as in the superficially different, but similarly stressful and unpredictable, conditions of the tropical seagrass communities. It may be, however, in view of the work of Sanders and Hessler (1969), who devised means of more adequately sampling deep-water environments, that the studies summarized by Kauffman (1967), which were carried out between 1913 and 1958, somewhat underestimated the diversity of the fauna associated with the cold-water thyasirids. The dominance of thyasirids in certain environments is probably real, but the faunal diversity of these environments may be greater than previously recognized.

In brief, at least some taxa of all three major lucinoid families apparently inhabit regions which are "marginal" in the sense that relatively few species are adapted to living there; but there is little evidence to support the earlier supposition that the Lucinacea as a group are competitively inferior to other eulamellibranch bivalves. In fact, they are able to exploit certain environments not open to most other eulamellibranchs. This revised view of lucinoid ecology changes one's perspective toward the evolution of the Lucinacea; for example, in an earlier paper I inferred that the dominance of lucinoids in marginal environments was a consequence of their competitive exclusion from more "desirable" environments by the supposedly more efficient Mesozoic eulamellibranchs (Bretsky, 1970). Certainly there are well-documented instances in the fossil record of environments dominated by one or a few lucinoid species. Excellent examples are provided by Kauffman (1967) and Speden (1965, 1970), both dealing with Upper Cretaceous assemblages from the Western Interior of the United States. Jackson (1970) stated that he found low-diversity lucinid-dominated assemblages in a presumably nearshore deposit in the middle Eocene of Jamaica. But the assumption that the dominance of marginal environments by lucinoids came about only after the Mesozoic radiation of infaunal eulamellibranchs was evidently unwarranted. McAlester (1963), for example, described an association from an Upper Devonian shale in Missouri whose fauna is roughly 75% lucinoid and 10% nuculoid. This shale is much more calcareous than contemporaneous clastic sediments from the Appalachian region in which lucinoids are unknown and infaunal, presumably filter-feeding bivalves are abundant. It appears likely, therefore, that early in their history lucinoid taxa inhabited environments which were inhospitable to many other bivalves.

If Early Paleozoic lucinoids were indeed already characteristic of marginal environments, it may be valid to suggest that, paradoxically, their adaptations to such environments, far from dooming them to ecological inferiority, actually accounted for their ability to diversify in the face of competition by new taxa of infaunal eulamellibranchs. Bretsky and Lorenz (1969) summarized a great deal of evidence from Recent ecological and genetic studies which suggests that organisms inhabiting unstable, fluctuating, and stressful environments tend to show a high degree of morphological and genetic diversity and thus are more readily able to adapt to sudden environmental changes than are organisms inhabiting stable environments, which do not set a high selective premium on morphological, behavioral, or genetic flexibility. Certainly the Recent lucinoid communities described by H. B. Moore, *et al.* (1968) and by Jackson (1970) seem to inhabit environments corresponding to the unstable regimes of Bretsky and Lorenz. These authors suggested that their model accounts for selective "mass" extinctions at the end of Permian time — those groups which became extinct had been adapted to more stable environments than had those which survived. J. S. Levinton (personal communication) remarked that most of the survivors of the Permo-Triassic crisis were also deposit feeders; whereas the lucinoids are apparently not deposit feeders in the sense that they actively search out detrital material, the larger species inhabiting unstable environments do feed on particles larger in size than those which can be utilized by most suspension feeders.

In summary, it is here postulated that at least some Paleozoic lucinoids may have inhabited marginal environments which were characterized by a high degree of environmental instability. Possessing a high degree of genetic or phenotypic plasticity, they were able to survive the Permo-Triassic crisis; and, possessing the basic eulamellibranch groundplan, they were able to exploit whatever circumstances in Mesozoic time brought about the eulamellibranch radiation. It seems most probable that the larger lucinoids tended to remain in physiologically stressful nearshore regimes, but that smaller species, which by their small size were not so amenable to life under rigorous conditions nor so well adapted to processing large food particles, became part of shelf communities which were highly diverse and which contained representatives of many eulamellibranch taxa. Probably most of the abundant small Tertiary lucinoids described by such workers as Clark and Martin (1901), Harris (1896, 1897, 1919, 1946), Gardner (1926, 1944), Woodring (1925) and Mansfield (1932, 1937) lived under normal-marine, relatively stable environmental conditions. The ungulinids, in particular, being anatomically closest to "typical eulamellibranchs", and, unlike the thyasirids and some lucinids, not having exploited cold waters, may prove to be especially characteristic of high-diversity communities [because faunal diversity generally is highest in tropical and subtropical shelf regimes (Sanders, 1968)].

## EVOLUTIONARY SIGNIFICANCE OF THE LUCINACEA

From his study of the anatomy of the Lucinacea, Allen (1958) inferred that, because the Ungulinidae are apparently most like other eulamellibranchs and the Lucinidae least so, with the Thyasiridae occupying an intermediate position (Table 1), "a series of evolutionary stages [could] be traced from the [Ungulinidae], which are closest to the primitive eulamellibranch, through the Thyasiridae to the extremely modified Lucinidae" (Allen, 1958, p. 480). As McAlester (1965, 1966) pointed out, this suggested evolutionary sequence is essentially just the reverse of the chronological order in which the three families appear in the fossil record. The first member of the Lucinidae found as a fossil is the Middle to Upper Silurian genus *Ilionia* Billings, 1875, found in eastern Canada and in Sweden. Specimens of *Ilionia* are usually preserved as internal molds which show a large, extremely elongate, curved anterior adductor scar and which usually also preserve an oblique line of gill attachment. The Thyasiridae are first known from Middle Triassic strata, and the Ungulinidae do not appear until the Upper Cretaceous (Chavan, 1969).

McAlester (1965, 1966) suggested that the anterior inhalant feeding current, rather than being a secondary specialization, is actually evidence for the primitiveness of the lucinoids. Yonge (1939) showed that in the earliest bivalves the pattern of water circulation was probably that found in the Recent protobranch *Nucula,* in which the water current enters anteriorly, passes over the gills, and exits posteriorly. The conjunction of an anterior-to-posterior water circulation with early appearance in the fossil record indicates that the Lucinacea are a primitive group.

The probable ancestor of the Lucinacea is the Middle Ordovician European bivalve *Babinka,* whose type species, *B. prima* Barrande, 1881, was described from Czechoslovakia. A number of students of molluscan phylogeny [see references in McAlester (1965)] noted that internal molds of specimens of *B. prima* preserve the impression of multiple pairs of muscle scars resembling those of fossil monoplacophorans and of the Recent monoplacophoran *Neopilina,* and proposed that *Babinka* might represent a transition between the Bivalvia and the Monoplacophora. After a restudy of Barrande's original material, McAlester (1964, 1965, 1966) concurred that the muscle pattern in *Babinka* appeared to have been inherited from an ancestor with monoplacophoran affinities. He suggested that the other characteristics of *Babinka* indicated a close similarity to the Lucinacea, though he considered it sufficiently distinct to be placed in a separate superfamily Babinkacea. The cardinal dentition of *Babinka,* with one large cardinal in the right valve and two slightly smaller ones in the left valve, is similar to that of many fossil and Recent lucinoids. The opisthodetic ligament, set in a narrow groove, and the long, narrow lunule also resemble those of undoubted lucinoids. The pallial line of *Babinka,* like that of the lucinoids, is nonsinuate. An elongate impression extending ventrally from the anterior adductor scar may have represented a specialized ciliary sorting area. *Babinka* thus probably was an infaunal suspension feeder with an anterior inhalant current. As in most lucinoids, also, the portion of the shell in *Babinka* anterior to the beaks makes up 50% or more of the total shell length. In the Lucinacea, the hypertrophy of the anterior adductor and the elongation of the foot require an expansion of the anterior portion of the shell, whereas in heterodont groups such as the Veneracea which have the same subround shell shape as the lucinoids, the greater portion of the shell is posterior to the beaks, to accommodate the siphons. Most students of the Bivalvia have accepted McAlester's evidence that *Babinka* is an ancestral lucinoid, although greater skepticism has been expressed concerning its direct derivation from the Monoplacophora (cf. Chavan, 1966; Newell, 1969; Pojeta, 1971).

The Lucinacea are sparsely represented in Paleozoic rocks. Chavan (1969) recognized seven Paleozoic lucinoid genera, allocating two to the Lucinidae, four to the Mactromyidae, and one to the Fimbriidae. Two of these are probably not lucinoids. The shape, dentition, and musculature of *Montanaria* Spriestersbach, 1909, as illustrated by Haffer (1959), are totally unlike those of any other lucinoid. Boss (1970) stated that the orginal figures of *Scaldia* de Ryckholt, 1847, which Chavan (1969) placed in the Fimbriidae, show a pallial sinus. The genera *Ilionia* Billings, 1875 (Silurian); *Paracyclas* Hall, 1843 (Silurian and Devonian); and *Phenacocyclas* LaRocque, 1950, are morphologically similar to Recent lucinoids. Figures which Chavan (1969) gave of *Palaeolucina* Chao, 1927, from the Mississippian of China, and of *Plesiocyprinella* Holdhaus, 1918, from the Permian of South America, are not particularly good, but attribution of lucinoid affinities to these genera does seem reasonable.

Chavan (1969) recognized two lucinoid genera from the Triassic of Europe and South America, placing one in the Thyasiridae and one in the Fimbriidae. Lucinoids are well represented in Jurassic and Cretaceous strata, the Mactromyidae and Fimbriidae being most common during the Mesozoic. The Lucinidae, Ungulinidae, and Thyasiridae become more important in Cenozoic time. All three of these families are now varied and numerically abundant throughout the world. The Thyasiridae are principally cold-water forms (Dall, 1901b; Kauffman, 1967); the Ungulinidae and Lucinidae have some cold-water representatives but are most common in tropical and subtropical seas (Dall, 1901b; Allen, 1958).

McAlester (1966) considered the Lucinacea an evolutionary dead end, believing that only one other higher taxon could be considered with any confidence to have descended from this group. This superfamily is the Leptonacea (= Erycinacea), comprising small commensal bivalves which have an anterior inhalant current and sometimes an elongate anterior adductor muscle (Leyborne Popham, 1940; Oldfield, 1955; Allen, 1968). They are first definitely known in early Cenozoic time (Chavan, 1969). Recently, Allen (1968) recorded striking similarities between the adaptations of the Lucinacea and those of the crassatelloid *Crassinella mactracea* (Linsley, 1845). *C. mactracea* has an anterior inhalant current and an elongated anterior adductor muscle. The structure of its palps and stomach are also similar to those of the Lucinacea. Stanley (1970) described the mode of life of another crassatellacean, *Astarte castanea* (Say, 1822), which lives with its anterior region uppermost and apparently draws water in anteriorly through the porous, gravelly substratum which it inhabits. These findings suggest a close relationship between the Lucinacea and the Crassatellacea, the superfamily from which all other nonlucinoid eulamellibranchs were probably derived (Stanley, 1968). There is, in fact, a Devonian genus, *Crassatellopsis* Beushausen, 1895, which appears to have lucinoid musculature but whose shape and dentition recall those of crassatelloids.

## MORPHOLOGY OF THE LUCINID SHELL

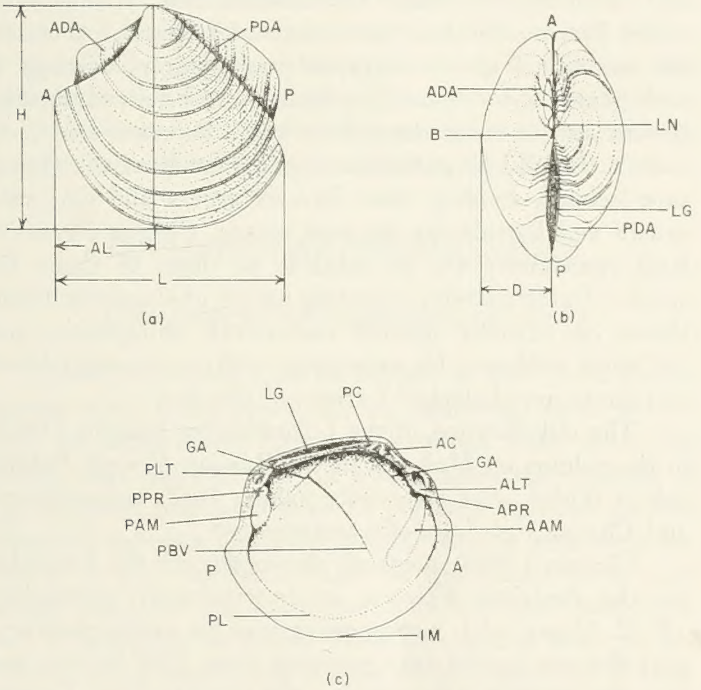
All previous classifications of the Lucinidae have been based almost entirely on features of the shell morphology. Studies of anatomy have necessarily been virtually restricted to those species which live intertidally or at depths readily accessible to divers. For example, Dall (1901b) listed 28 Recent lucinids from the West Indies. Allen (1958), collecting in shallow water in Florida and the Bahamas, was able to study six of these. Stanley (1970), collecting in Florida and Puerto Rico with the aid of SCUBA equipment, observed four of these same species and two others not studied by Allen. Thus only about a third of the species described from one of the best-known and most accessible regions where lucinids are common could be considered to be easy to collect alive.

Taxonomists who have tried to formulate classifications which would be applicable to both fossil and living Lucinidae have of necessity emphasized those characters which can be determined for all the species studied. For similar reasons, the present study also emphasizes shell characters. When characters were recorded for my numerical-taxonomic investigation, only shell characters could be used because, in the calculation of phenetic resemblances, the coefficients of similarity may be misleading unless nearly all the characters used are possessed by nearly all the organisms in the study (Sokal and Sneath, 1963, p. 165). Anatomical data from Allen (1958) were available for only eight of the species included in the phenetic study. In the discussions of inferred relationships I have used whatever evidence from soft-part morphology seemed relevant, but certainly the greater part of the phylogenetic interpretations presented here are based on shell morphology.

Text-figure 2, which represents a generalized lucinid, illustrates the major features of lucinid shell morphology. The average length of the shell varies widely, from less than 5 mm in *Lucina (Parvilucina) multilineata* Tuomey and Holmes to more than 100 mm in *Anodontia (Anodontia) philippiana* (Reeve) and *Codakia (Codakia) distinguenda* (Tryon). Lucinid shells are slightly longer than high; in inflation they range from globose to strongly compressed. The shell is usually white, though in some tropical forms the shell interior is pink, orange, or yellow. The periostracum is generally thin or absent, except in cold-water forms, which usually have a heavy brown periostracum.

Surface sculpture in the Lucinidae is variable. It is usually concentric, either of irregularly spaced lines of growth or regularly spaced lamellae, or both; many species also have radial sculpture. Concentric and radial sculpture may be equally strong, producing a cancellate pattern of surface sculpture; or one or the other may predominate. Some species have only a few (2 to 12) broad radial ribs, but most radially sculptured species have 20 or more thin radial ribs. Some species have divaricate sculpture, in which lines running obliquely to the concentric growth lines meet in an obtuse angle on the anterior part of the shell (*e.g.,* Pl. 36, fig. 7).

The line of gill attachment is usually marked anteriorly and posteriorly by distinct lines on the interior of the shell. Externally, the posterior line often marks off a distinct posterodorsal area, sometimes also producing a notch in the posteroventral margin of the shell (*e.g.,* Pl. 27, fig. 1). There may be no distinctly impressed external line, but the surface sculpture on the posterior part of the shell may be different from that on the rest of the shell. Usually the anterior line of gill attachment is more faintly reflected externally, generally by a slight change in surface sculpture. There may, however, also be a distinctly set off anterodorsal area, marked by an impressed line, sunken below the level of the beaks, and oval or heart-shaped. These *anterior* and *posterior dorsal areas* (Dall, 1901b, 1903) may resemble the lunule and corselet of other bivalves, but they are functionally different [cf. Allen (1958), Carter (1967a)].



Text-figure 2. Morphology of the shell of a generalized lucinid. a. Exterior of left valve. b. Top view of articulated shell, showing relationships between dorsal areas, lunule, and ligament. c. Interior of left valve.

Key to symbols: A, anterior; AAM, anterior adductor muscle scar; AC, anterior cardinal tooth; ADA, anterior dorsal area; AL, anterior length; ALT, anterior lateral teeth; APR, anterior pedal retractor scar; B, beak; D, depth of one valve; GA, trace of gill attachment on interior of shell; H, height of shell; IM, inner margin of shell; L, length of shell; LG, ligament; LN, lunule; P, posterior; PAM, posterior adductor muscle scar; PBV, pallial blood vessel scar; PC, posterior cardinal tooth; PDA, posterior dorsal area; PL, pallial line; PLT, posterior lateral teeth; PPR, posterior pedal retractor scar.

The lucinids do have a small sunken area in front of the beaks which can properly be called a lunule. It is deeper and considerably smaller than the anterior dorsal area. In shape it may be short and triangular or round; or long, narrow, and oval or rectangular. It is often formed by a projection in one valve which fits into a recess in the opposite valve. The lunule may be deeply impressed into the hinge plate, forming a circular depression or one shaped like an infinity sign (Pl. 26, fig. 4) and partly or totally obliterating the anterior cardinal tooth. In a few species, such as *Lucina (Lucina) pensylvanica* (Linné), the lunule is clearly defined only on young specimens.

The elongate anterior adductor muscle is the most prominent feature of the interior of the lucinid shell. The anterior and posterior muscle scars are usually about equal in width, but in a few species the anterior adductor is much narrower than the posterior one. The posterior adductor scar lies at the posterodorsal termination of the pallial line, which if extended would approximately bisect the scar. The posterior scar, almost always considerably shorter than the anterior one, is round or elliptical. The anterior and posterior pedal retractors usually lie just above the corresponding adductors. The anterior retractor scar is usually completely separate from that of the anterior adductor, but the posterior pedal retractor scar is partly or completely fused with that of the posterior adductor. Most lucinids also have a diagonal impression across the shell interior; this is best developed in the thicker-shelled species, and in some species is seen only on the larger shells. This line appears to mark the position of a pallial blood vessel, which transports blood from folds in the inner mantle (mantle "gills") to the auricle (Allen, 1958, pp. 429-432, figs. 3, 4).

The dentition of the Lucinidae is variable. In its maximum development, the dentition is as follows: two cardinals in each valve, an anterior and a posterior lateral in the right valve, and double anterior and posterior laterals in the left valve. The right anterior cardinal is usually smaller than the right posterior one. Some species have the cardinals almost completely effaced; others lack laterals but have strong cardinals; and a few species are edentulous.

The ligament is opisthodetic. It is usually long, narrow, and external. Some genera, such as *Codakia,* characteristically have a shorter, broader ligament which is inset in a deep groove. In one genus, *Loripes,* the ligament is made up of a reduced external portion and a conspicuous internal portion which are almost completely separate (Allen, 1960).

## PREVIOUS TAXONOMIC STUDIES OF THE LUCINIDAE

Lucinids were among the first bivalves to enter into the formal system of nomenclature, because some species were described by Linné (1758) as part of his genera *Venus* and *Tellina.* The first lucinid to receive a separate generic name was a supposedly Senegalese shell first described by Adanson (1757) as *"Chama, le codok"*. Scopoli (1777) gave this species the generic name *Codakia.*

Bruguière (1797) introduced the name *Lucina* at the top of three plates of *Encyclopédie Méthodique.* Bruguière died before completing the descriptions which were to accompany this work (Dance, 1966); thus he never formally described the genus or identified the species which he included in it. Lamarck (1799, 1801) was the first to describe the genus; in each description he cited as an example of *Lucina* a different one of the species represented by Bruguière's figures, but neither citation accords with the rules for type designations set forth in the current code of zoological nomenclature. The choice of a type species for *Lucina* is a complicated matter [cf. Stewart (1930); Chavan (1937, 1952a)]; it is reviewed in the discussion of *Lucina* in the section on systematics. Chavan and Stewart reach different conclusions, both of which disagree with the interpretation by Dall (1901b) which considered the citation by Lamarck (1799) a valid type designation, a reasonable conclusion at that stage of the development of nomenclatural rules. In this study I have accepted Stewart's viewpoint which makes *Venus pensylvanica* Linné the type species of *Lucina.*

Nineteenth-century taxonomy centered upon the discovery and description of new species and genera. By 1900, 24 genera and several hundred species of Lucinidae had been described. The American malacologist and paleontologist William Healey Dall was one of the first to apply evolutionary principles to the classification of the Mollusca. In 1901, he published a synopsis of the Recent American species of the Lucinacea, one of a series of synopses of various groups of the Bivalvia. His classification of the Lucinidae comprised only six genera, but he divided these genera into a large number of subgenera and sections (a category which he employed as a subdivision of a subgenus), some of which unfortunately he described so briefly that their definition is intelligible only by recourse to the specimens which he studied.

Dall's (1890-1903) monumental *Tertiary Fauna of Florida* was a taxonomic and evolutionary study of every family of gastropods and bivalves represented in the Floridian Tertiary. Dall emphasized the evolutionary basis of classification, incorporating both stratigraphic and morphological evidence into his evolutionary scheme. He also stressed the importance to the study of fossils of an understanding of the anatomy of living representatives of the group. Though some of Dall's generic assignments may be erroneous and some of his evolutionary hypotheses must be modified because of changed ideas on certain of his stratigraphic correlations, his work remains fundamental to any study of the evolution of American Bivalvia.

Several other studies similar in scope to Dall's followed. Lamy (1920) in a revision of the Recent Lucinacea in the collections of the Muséum national d'Histoire naturelle, Paris, used Dall's classification in a study of the Recent lucinoid fauna of the world. His work is especially notable for its species-level synonymies.

Chavan (1937, 1938) studied both fossil and Recent Lucinidae, except for those with divaricate sculpture, from all parts of the world. He discussed the nomenclatural problems involved in choosing the type species for several lucinid genera; modified Dall's classification to divide the Lucinidae into 13 genera, most of which had from two to six subgenera; and traced the evolution of the Lucinidae from Jurassic time to the Recent, with brief discussions of Paleozoic Lucinidae. He established the stratigraphic and geographic range of each genus and subgenus by listing and briefly discussing the occurrence of all the species which he considered it to include. In 1951 he published a similar study of the divaricate lucinids, dividing them into six genera and nine subgenera and introducing six new names. Chavan's generic-level synonymies are as valuable as those of Lamy for species. Unfortunately, in setting up his phylogenetic hypotheses he virtually ignored anatomical, ontogenetic, and ecological evidence; his taxonomy is often tenuously based on minute morphological features of the shell.

The classification of the Lucinidae by Eberzin (1960) in the volume on Mollusca in the Russian *Osnovy Paleontologii* (Orlov, ed.) essentially follows Dall's nomenclature and Chavan's phylogenetic arrangement.

Chavan (1969) prepared the section on the Lucinidae for the American *Treatise on Invertebrate Paleontology* (R. C. Moore, ed.), incorporating into his earlier classification the new lucinid taxa proposed since 1938 by him and by other workers. Of necessity, the format of the *Treatise* does not permit detailed documentation of proposed classifications, and in some cases it is difficult to understand the basis on which changes have been made in Chavan's earlier classification.

Table 2 presents a comparison of Chavan's (1969) classification of the Lucinidae and that proposed here. My classification includes a number of taxa not represented in the phenetic study — either because specimens were not available for study, or because specimens which were available were not well enough preserved to provide a sufficiently large number of characters. I have not attempted to classify all the genus-group taxa recognized by Chavan, because in a number of cases I have seen neither representative specimens nor well-done figures. Chavan divided the Lucinidae into four subfamilies; the highest taxon which I have used is the genus. I consider it generally preferable to employ a few broadly defined genera which nonspecialists can easily recognize, sacrificing some finer details of phylogeny which seem better represented graphically or descriptively rather than taxonomically. In both Chavan's classification and mine as presented in Table 2, the linear order of taxa roughly corresponds to a phylogenetic arrangement. Because Chavan and I disagree about the application of the name *Lucina* and *Phacoides,* to facilitate comparison of the classifications I have, in presenting Chavan's version, employed the names in a manner consonant with my interpretation of what the type species of *Lucina* is, placing the names which Chavan actually employed in brackets. Names in parentheses are considered junior synonyms of the name which they follow; a question mark before the equals sign indicates that the synonymization is not certain. Question marks before the names of taxa indicate that the placement of the taxon in a particular subfamily or genus is not certain.

## PHYLOGENY OF THE LUCINIDAE

### AVAILABILITY OF PHYLOGENETIC DATA

Three conditions must be fulfilled in order for a phylogenetic study based principally on fossil evidence to be carried out successfully. First, the localities from which the faunas were collected and the stratigraphic relationships of the enclosing sediments must be precisely recorded so that temporal sequence and biogeography can be accurately assessed. Second, the fossils must be well preserved so that a large sample of the total number of hard-part characters will be available for study. Third, the faunas must be accessible for personal study by the worker interested in their phylogenetic relationships.

In this study, the three conditions outlined above are most nearly fulfilled for the Cenozoic record of the eastern and southern United States. Of primary importance, of course, is the fact that Tertiary and Pleistocene fossil forms can be readily compared with analogous Recent species, and inferences about anatomy, functional morphology, and physiology can be made with considerable confidence. In this geographic area, also, stratigraphy and structure are relatively simple. The Cenozoic history of the Atlantic Coast and Gulf Coast states has been primarily one of marine regression, so that the exposed formations generally are progressively younger seaward. There has been little tectonic activity. The faunas are well preserved because many of the sediments, particularly the sands, are barely consolidated. The molluscan fauna has been extensively studied for over 125 years, and a number of comprehensive monographs of the mollusks of particular states or formations have been written. Because nearly all the taxonomists who have studied the Atlantic Coast and Gulf Coast fauna were associated with one or more of the major Eastern museums, their collections were conveniently accessible. Many of these taxonomists had also worked with the Cenozoic Mollusca of the West Indian islands and the Central American and South American shores of the Gulf of Mexico and the Caribbean, increasing the knowledge of the probable ancestry of the species now inhabiting these seas.

The fossil and Recent fauna of western North America is clearly related to that of the western Atlantic and Caribbean, because these areas were connected by seaways throughout most of Cenozoic time. The Cenozoic history of the West Coast, however, has included much tectonic disturbance. Structural complexities result in considerable uncertainty about correlations within the area, and there is even less agreement about correlations with eastern North America and Europe. Completely different local time subdivisions are recognized, in fact, by workers specializing in vertebrates, in the larger invertebrates, and in microfossils (Durham, 1954). The West Coast bivalves, generally more poorly preserved and more strongly affected by tectonic deformation than their East Coast counterparts, have accordingly been less attractive to monographers. Most species were named and described as an adjunct to stratigraphic studies. The principal work on the taxonomy of West Coast fossil mollusks, a compilation by Grant and Gale (1931), deals mostly with late Tertiary forms. Little systematic work has been done on the more difficult, more poorly preserved early Tertiary mollusks. Many West Coast lucinids are included in the present study, and their most probable affinities are indicated. For a number of species based on material deposited in West Coast museums, however, only tentative generic or subgeneric assignment was attempted, pending study of the original material. For all these reasons, information contributed by the faunas of western North America about the Cenozoic evolution of the Lucinidae is less reliable than that based on species from eastern North America.

## TABLE 2

### COMPARISON OF THE CLASSIFICATIONS OF CHAVAN (1969) AND OF THIS PAPER

| CHAVAN (1969) | THIS PAPER |
|---|---|
| Subfamily Lucininae | |
| Phacoides [Lucina] | Lucina |
| Phacoides (=Egraca, =Dentilucina) | Lucina (=Linga, =Egraca, |
| Lucinisca | ?=Dentilucina) |
| Recurvella | Here |
| Volupia | Herella |
| Here | Illesca |
| Here | Volupia |
| Herella | Phacoides (=Dentilucina) |
| Lucina [Linga](=Quasilucina) | Stewartia |
| Lucina (=Lepilucina) | Lepilucina |
| Illesca | ?Megaxinus |
| Pleurolucina (=Dallucina, | Callucina |
| =Paslucina) | Callucinopsis |
| Bellucina (=Cardiolucina) | Pseudolucinisca |
| Parvilucina | Parvilucina |
| Parvilucina | Callucinella |
| Cavilinga | Cavilinga (?=Cardiolucina) |
| Microloripes | Cavilucina |
| Callucinella | Bellucina |
| Callucina | Lucinisca |
| Callucina | ?Barbierella |
| Pseudolucinisca | Pleurolucina (=Dallucina, |
| Striolucina | =Paslucina) |
| Callucinopsis | Recurvella |
| Barbierella | Mesolinga |
| Pillucina | Luciniola |
| Pillucina | ?Phenacocyclas |
| Sydlorina | ?Crassatellopsis |
| Wallucina | |
| Loripes (=Lucinida) | Codakia |
| Nevenulora | Codakia (=Lentillaria, |
| Nevenulora | =Antilla, =Pexocodakia) |
| Jagonoma (=Dilora) | Epicodakia |
| Megaxinus (=Stewartia) | Talocodakia |
| Megaxinus | Ctena |
| Pteromyrtea | ?Claibornites |
| Ctena | ?Jagonoma |
| Ctena | |
| Talocodakia | |
| Epicodakia | |
| Luciniola | |
| Codakia (=Lentillaria, =Antilla, | |
| =Pexocodakia) | |
| Codakia | |
| Epilucina | |
| Cavilucina | |
| Mesolinga | |
| Subfamily Myrteinae | |
| Mesomiltha | Miltha |
| Monitilora | Miltha (=Milthoidea) |
| Monitilora | Recticardo |
| Prophetilora | Eomiltha |
| Gonimyrtea (?=Levimyrtaea) | Gibbolucina |
| Myrtea (=Cyrachaea, =Eulopia, | Plastomiltha |
| ?=Notomyrtea) | Lucinoma (?=Gonimyrtea) |
| Myrtea | Armimiltha |
| Myrteopsis (?=Levimyrtaea) | Pseudomiltha |
| ?Perampliata | ?Saxolucina |
| Gardnerella | ?Codalucina |
| Milthona | ?Mesomiltha |
| Lucinoma | ?Discomiltha |
| Discomiltha | ?Ilionia |
| | ?Paracyclas |
| Subfamily Milthinae | |
| Phenacocyclas | Myrtea |
| Pterolucina | Myrtea (=Cyrachaea) |
| Myrtucina | Notomyrtea |
| Jagolucina | Eulopia |
| Saxolucina | Myrteopsis (?=Levimyrtaea) |
| Saxolucina | ?Epilucina |
| Plastomiltha (=Armimiltha) | ?Myrtucina |
| Claibornites | ?Nymphalucina |
| Claibornites | |
| Codalucina | |
| Miltha (=Milthoidea) | Anodontia |
| Miltha | Anodontia (=Pegophysema, |
| Recticardo | =Prophetilora, =Lisso- |
| ?Trinitasia | sphaira) |
| Ilionia (=Prolucina, =Platymermis) | Eophysema |
| Gibbolucina (?=Elathia) | ?Gardnerella |
| Gibbolucina | |
| Eomiltha | Loripes |
| Pseudomiltha | Loripes (=Lucinida) |
| Pseudomiltha | Loripinus |
| Zorrita | Pillucina |
| Eamesiella | Wallucina |
| Pegophysema | Sydlorina |
| Pegophysema (=Lissosphaira) | Microloripes |
| Eophysema | |
| Anodontia | |
| Anodontia | |
| Cavatidens | |
| Loripinus | |
| Subfamily Divaricellinae | |
| Divalinga | Divaricella |
| Divalinga | Divaricella |
| Viaderella | Egracina |
| Stchepinskya | Divalinga |
| Paralucinella | Viaderella |
| Lucinella | Stchepinskya |
| Divalucina | Paralucinella |
| Boeuvia (?=Bourdotia) | Lucinella |
| Divaricella | Divalucina |
| Divaricella | Boeuvia (?=Bourdotia) |
| Egracina | Pompholigina |
| Pompholigina | Eodivaricella |
| Pompholigina | |
| Eodivaricella | |

Data on European lucinids have been largely taken from the work of Chavan, spanning over thirty years. My knowledge of the European species is limited by my having seen little European fossil material, and no type specimens of European lucinid species. Because Chavan has also studied many of the North American forms included in the present work, it is usually readily possible to compare his and my concepts of the various genera and subgenera. In nearly every instance, the phylogenetic trends which he outlined for European lucinid species are closely paralleled in the North American ones. The similarities between the European and North American Lucinidae are consistent with the evidence from many fields of study that the eastern and western Atlantic coasts formed essentially a single faunal province until near the end of Tertiary time [see Ekman (1953); Adams and Ager, eds. (1967)]. Chavan's work on the European lucinids is, of course, founded on over one hundred fifty years' accumulated data on European fossil Mollusca, particularly well known from areas such as the Paris Basin where there are few structural complications.

Knowledge of the Cenozoic evolution of the Lucinidae is most complete for North America and Europe. Information from some other area was incorporated into this study. The Tertiary Mollusca of South America have been the subject of a number of studies by Olsson. His collections, most of which are deposited in the Paleontological Research Institution, were available for study. Though further work on the biostratigraphy of the South American marine deposits may alter some of his age assignments, these studies of the South American species have contributed much toward establishing the geographic ranges of a number of lucinid groups.

In the Indo-Pacific region, the best-known Cenozoic molluscan faunas are those of Australia, New Zealand, and Japan. Again, inaccessibility of specimens has limited the incorporation of information on these faunas into the present study. Earlier workers have accorded generic or subgeneric rank to several distinctive fossil and Recent lucinids from the Indo-Pacific region. In some cases the relationships of these taxa to North American and European Lucinidae are clear; in other groups, more intensive study is necessary to determine affinities.

Knowledge of the pre-Cenozoic evolution of the Lucinidae is limited almost entirely to North America and Europe. Problems of deformation, poor preservation, and loss of the record by erosion are likely to be accentuated the farther back one goes in time. Mesozoic lucinids are common in only a few localities; one example is the North American *Myrtea*? *(Nymphalucina) occidentalis* (Morton, 1842), which forms monospecific associations in Upper Cretaceous rocks of the Western Interior. Lucinids have also been described from some Upper Cretaceous localities in the Gulf Coast area (Stephenson, 1941, 1952). Though most are rare and too poorly preserved for determination of their generic affinities, some seem clearly related to phyletic lines which are well developed in Tertiary time. In Europe, a classic locality for lucinids is the Upper Jurassic (Sequanian) Glos sands of Cordebugle, Calvados, France, from which about ten lucinid species have been described (Zittell and Goubert, 1861; Chavan, 1952b). Most of the lineages which can be recognized in Cenozoic lucinids seem already to be represented at the Jurassic locality. As Chavan (1952b) noted, suggestions of possible relationships must be speculative because of the lack of forms intermediate between the Jurassic species and those of Late Cretaceous or early Tertiary age. In this study, a further difficulty is my not having examined specimens of the Cordebugle lucinids.

A few Triassic forms have been referred to the genus *Lucina,* but they are generally based on specimens of which no internal features are known. Apparently no Pennsylvanian lucinids have ever been noted. The Permian *Plesiocyprinella* Holdhaus, 1918, is probably correctly placed in the Mactromyidae (Chavan, 1969). The Mississippian *Palaeolucina* Chao, 1927, from mainland China, may belong to the Lucinidae, but the original figures are too poor to suggest its affinity to any of the major subdivisions of this family, and chances of examining original specimens are small. Devonian lucinids are fairly abundant but generally poorly preserved; the few Silurian forms usually occur only as internal molds. Knowledge of the Lucinidae of both periods is again based almost entirely on North American and European forms. The absence of stratigraphic intermediates makes it inadvisable to attempt to draw any firm conclusions about the relationships between Paleozoic and later lucinids.

Because of the limitations outlined above, this study is not presented as a complete phylogeny of the Lucinidae but simply as an attempt at constructing an evolutionary framework. The next section outlines the methods by which that framework was established.

## METHODS OF INFERRING PHYLOGENY

As advocates of the phenetic approach to classification rightly point out, all phylogenetic hypotheses are based on evaluation of the degree of morphological similarity between specimens. Knowledge of the temporal relationships of faunas sets bounds to phylogenetic speculation and frequently permits choice among alternative phylogenetic reconstructions which from morphological evidence alone seem equally tenable. Knowledge of biogeography and paleoecology can suggest factors controlling evolutionary trends, radiations, and extinctions, and can explain similarities among faunas of areas now separated by physical or climatic barriers, or anomalous discontinuities in distribution. Ultimately, however, phylogenetic relationships must be inferred from morphological resemblances.

The phylogenetic reconstruction presented here was carried out as follows: I selected the species to be used in the phenetic study according to the criteria noted in the introduction. Table 3 lists these species. The taxonomic assignments are those proposed in this study. Taking each of the species in the phenetic study in turn as a starting point, I listed first the species contemporaneous with it which resembled it most closely, and then recorded their resemblances to species from successive time horizons. Beginning with a Recent species, for example, I first considered other living species which closely resembled it; then I compared the Recent species to those of the Pleistocene; the Recent and Pleistocene species to Pliocene ones; the Recent, Pleistocene, and Pliocene ones to those of the Miocene; and so forth. The same procedure was followed with a fossil species as the starting point, except of course that it was necessary to work both forward and backward in time. In this way it was possible to recognize chains of closely similar species. Many distinctive morphological groups eventually disappeared from the record, and a number of early forms were found which were similar to two or more of the later groups. In this way the duration of phyletic lines and their probable ancestry could be established. The comparisons were facilitated because most of the species chosen for the phenetic study are type species of genera, subgenera, or "sections," and the authors of these taxa had in most cases enumerated the species which they considered the new taxon to include. I also relied strongly on the work of Lamy (1920) and Chavan (1937, 1938, 1951a, 1952b) for evaluation of the relationships between North American Recent and fossil species and their counterparts in Europe and other areas. Whenever possible I examined the original published descriptions and figures of species mentioned by Lamy and Chavan but deposited in collections other than those to which I had access. A tentative assessment of the generic and subgeneric placement of these taxa was thus possible.

Accuracy of phylogenetic reconstruction is closely linked to accuracy of correlation. European geologists divide each of the Tertiary epochs into from two to six stages. In eastern North America, only a twofold or threefold subdivision of each epoch is generally accepted; the definition of these in terms of the European stages is generally well worked out but involves some boundary problems. In the western United States, as previously noted, correlation with the standard sections of the East Coast and of Europe is more difficult and varies according to whether microfossils or megafossils are used as criteria (Weaver, *et al.*, 1944; Durham, 1954). For these reasons, dates for the North American fossil species can usually be given only in such terms as early, middle, or late Miocene. Sometimes the maximum accuracy possible is assignment to the proper epoch. Because Pliocene and Pleistocene analogues of most Recent bivalve species are only subspecifically distinct from the living forms, for the purpose of this study it was not necessary to attempt to determine the correlation of Pleistocene strata from which lucinids were collected with the various interglacial stages, and it was possible to consider all of Pliocene time as a unit.

Accepting the time scale of Harland, Smith, and Wilcock (1964), which placed the beginning of Pliocene time at about 7 million years before the present, and assuming that most Recent lucinid species have existed in nearly their present form since late Miocene or early Pliocene time, a reasonable estimate of the minimum duration of a lucinid species is about 4 to 8 million years. If correlations are accurate enough to place formations and their included species within the proper half or third of each of the pre-Pliocene Tertiary epochs, these subdivisions are of about the same length as the expected duration of a species. [Harland, Smith, and Wilcock gave the duration of the Miocene epoch as 19 million years; Oligocene, 12 m. y.; Eocene, 16 m. y.; and Paleocene, 11 m. y. Most North American correlation charts, following Cooke, Gardner, and Woodring (1943), recognize two Paleocene stages and three for each of the other epochs. Assuming that the subdivisions of each epoch divide it about equally, the length of each stage ranges from about 4 to about 6.3 million years.] For this study, therefore, which attempts to determine the relationships among species rather than the course of evolution within species, a reasonably close approximation to a continuous record of evolution is available, at least for eastern North America and Europe. Of course, many species may not have been preserved as fossils; much of the record may have been destroyed by erosion; and many species, particularly deep-water ones, may be inaccessible for study because the enclosing strata have never been exposed subaerially. Considering all these limitations, the Cenozoic record of the Lucinidae is still sufficiently complete to justify inferring that closely similar specimens in, for example, a middle Eocene and a late Eocene deposit were connected through time by a chain of intermediate forms.

Before Pliocene time, when the marine faunas of the eastern and western coasts of North America and South America were still in communication through the Panamanian region, and the Atlantic, Indian, and western Pacific Oceans were interconnected through the Tethys Sea, the time required for worldwide dispersal of a species, or at least of a succession of closely related species, must in most cases have been almost negligible given the limits of resolution of the present geologic time scale. For this reason it is not generally possible to trace migration routes for the various lucinid groups; but little error is introduced by considering two closely similar forms of the same age, one from Europe and one from North America, as samples of the same gene pool. In short, the "imperfections of the geological record" should not greatly detract from the validity of the scheme here presented of the Tertiary evolution of the Lucinidae.

Age assignments here given for specific Cenozoic formations in North America generally follow the correlation charts of Cooke, Gardner, and Woodring (1943), for the Atlantic and Gulf Coastal Plain, and of Weaver, *et al.* (1944), for western North America. Modifications suggested by later workers are summarized by Murray (1961) and Richards (1967) for the southern and eastern United States, and by Durham (1954) for southern California. Gignoux (1955) was the principal reference for European correlations. For areas not covered by these compendia, I have accepted the age assignment indicated by the worker whose study is cited. For many of the Central American and South American faunas described in the early twentieth century, age assignments were usually based on correlation with formations of the eastern United States, some of which have since had their dates modified. In such cases, I have considered the original correlation of the Latin American formation to have been correct, making the implicit change in its age assignment.

## THE LUCINID LINEAGES

From the evidence gathered as outlined above, it has been possible to allocate the species of the phenetic study and their probable relatives among seven discrete groupings. Five of these, which appear to represent monophyletic taxa, will be referred to as *lineages*. The other two are not well represented in the North American fossil record. Because in these cases I was uncertain whether all the European and Indo-Pacific species considered by Chavan (1937, 1938, 1951a) most closely related to the species included in the phenetic study indeed had a common ancestry with them, I have used the term *group* for these possibly polyphyletic taxa. Each of the major lineages and groups is given generic status, and clusters of closely related species are treated as subgenera. It is difficult to determine the relationships among the various genera, because all but one are known by the beginning of Cenozoic time, and most are evidently represented in the Jurassic. The genera recognized here, and their probable durations, are as follows:

*Lucina* lineage—Devonian? Jurassic-Recent
*Codakia* lineage—Jurassic-Recent
*Miltha* lineage—Silurian? Jurassic-Recent
*Myrtea* lineage—Jurassic? Cretaceous-Recent
*Anodontia* lineage—Paleocene-Recent
*Loripes* group—Paleocene-Recent
*Divaricella* group—Cretaceous-Recent

Though the first five genera are probably monophyletic, each, of course, includes some species and subgenera whose generic position cannot be unequivocally decided on the basis of present knowledge. A summary of the characteristics and history of the several lucinid lineages and groups follows. More detailed evidence and documentation, and complete references to the taxa discussed, are given in the section on systematics in the discussion of the distribution and phylogenetic relationships of each subgenus. The species included in the phenetic study are discussed in detail in the section on systematics, in an order corresponding to that in which they are listed in Table 3.

Relative size terms used in the generic diagnoses and specific descriptions in this paper are defined as follows:

Very small—adult length less than 1 cm
Small—adult length 1-2 cm
Medium—adult length 2-4 cm
Large—adult length 4-8 cm
Very large adult length greater than 8 cm

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On both stratigraphic and paleontologic evidence (mollusk, Foraminifera, ostracodes) formations such as Yorktown, Duplin, Pinecrest of the Atlantic Coastal Plain, formerly considered as late Miocene in age, are assigned to the Pliocene by several prominent specialists. The same high Tertiary age (Pliocene) is assigned on good paleontological evidence to several fossiliferous formations in the Caribbean region, formerly believed to be Miocene, such as the Limon beds of Costa Rica, the Chagres of Panama, and the Bowden of Jamaica. A. A. Olsson, Aug. 16, 1976.

## TABLE 3

### SPECIES INCLUDED IN THE PHENETIC STUDY

*Lucina (Lucina) pensylvanica* (Linné, 1758)
*Lucina (Here) excavata* Carpenter, 1857
*Lucina (Phacoides) pectinata* (Gmelin, 1791)
*Lucina (Stewartia) anodonta* Say, 1824
*Lucina (Stewartia) floridana* Conrad, 1833
*Lucina (Callucina) radians* Conrad, 1841
*Lucina (Callucina) papyracea* Lea, 1833
*Lucina (Parvilucina) tenuisculpta* Carpenter, 1864
*Lucina (Parvilucina) multilineata* Tuomey and Holmes, 1857
*Lucina (Parvilucina?) costata* d'Orbigny, 1842
*Lucina (Cavilinga) trisulcata* Conrad, 1841
*Lucina (Cavilinga) pomilia* Conrad, 1833
*Lucina (Cavilinga) lingualis* Carpenter, 1864
*Lucina (Cavilinga) lampra* (Dall, 1901)
*Lucina (Bellucina) amiantus* (Dall, 1901)
*Lucina (Lucinisca) nassula* Conrad, 1846
*Lucina (Lucinisca) nuttalli* Conrad, 1837
*Lucina (Pleurolucina) leucocyma* Dall, 1886
*Lucina (Pleurolucina) undatoides* Hertlein and Strong, 1945
*Lucina (Pleurolucina) amabilis* Dall, 1898
*Lucina? (Recurvella) dolabra* Conrad, 1833
*Codakia (Codakia) orbicularis* (Linné, 1758)
*Codakia (Codakia) distinguenda* (Tryon, 1872)
*Codakia (Ctena) mexicana* Dall, 1901
*Codakia (Ctena) orbiculata* (Montagu, 1808)
*Codakia? (Claibornites) symmetrica* (Conrad, 1833)
*Miltha (Miltha) xantusi* (Dall, 1905)
*Miltha (Eomiltha) pandata* (Conrad, 1833)
*Miltha (Plastomiltha) claibornensis* (Conrad, 1865)
*Miltha (Lucinoma) filosa* (Stimpson, 1851)
*Miltha (Armimiltha) disciformis* (Heilprin, 1887)
*Myrtea (Myrtea) spinifera* (Montagu, 1803)
*Myrtea (Eulopia) sagrinata* (Dall, 1886)
*Myrtea (Myrteopsis?) lens* (Verrill and Smith, 1880)
*Myrtea? (Epilucina) californica* (Conrad, 1837)
*Anodontia (Anodontia) alba* Link, 1807
*Anodontia (Anodontia) philippiana* (Reeve, 1850)
*Anodontia (Eophysema) subvexa* (Conrad, 1833)
*Loripes (Loripes) lacteus* Poli, 1791
*Divaricella (Divalinga) quadrisulcata* d'Orbigny, 1842
*Divaricella (Divalinga) eburnea* (Reeve, 1850)
*Divaricella (Egracina) dentata* (Wood, 1815)

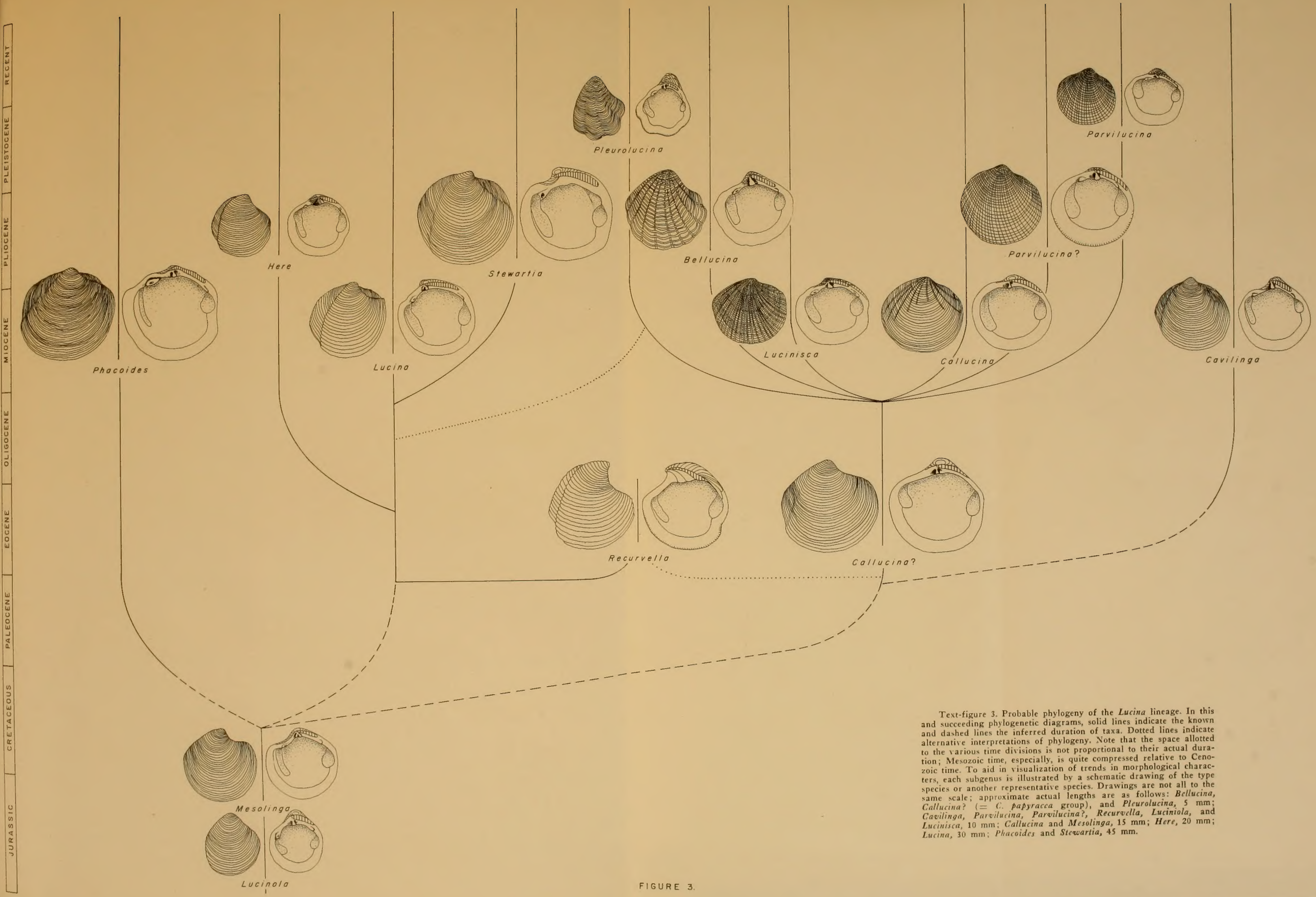
### THE LUCINA LINEAGE

This is a difficult taxon to characterize morphologically, because it includes among its diverse species a variety of combinations of sculpture, dentition, lunule type, and musculature. Characters which are constant in one subgenus may be variable from species to species but constant within each species of another subgenus, and may vary within some or all the species of a third. In almost every case, however, the subgenera referred to the *Lucina* lineage can be shown to be related to each other through stratigraphic and morphological intermediates.

*Diagnosis of the genus Lucina.* — Shell of very small to medium size, thickness usually moderate, ranging from slightly longer than high to considerably higher than long, but generally rounded (H/L ratio usually about 0.95-1.05), generally moderately to strongly inflated, anterior expansion usually moderate. Surface sculpture concentric or both concentric and radial, fine to coarse; concentrics generally all of equal prominence except for growth rings which are usually irregularly spaced; growth rings lacking in some species, most commonly those with radial as well as concentric sculpture, or with two orders of concentric ribs (widely spaced, elevated concentrics with several fine, closely spaced lamellae between). Number of radials, where present, varying from 2 to 20 or more; radial ribbing variable in prominence relative to concentrics, in degree of bifurcation, in relative strength on different parts of shell, and in whether or not depressions between radial ribs are sufficiently deep to produce an undulatory shell surface. Dorsal areas faint to conspicuous; anterior one may form pseudo-lunule or may be defined only by change in sculpture; posterior one may bear spines on dorsal margin. Shell interior or exterior, or both, may bear color; periostracum, when present, thin and flaky. Lunule length, width, shape, degree of asymmetry, depth, and distinctness all variable; deeply excavated lunule present only in this genus. Ligament external or only slightly inset, narrow, extending across almost all of area between beak and posterior margin of shell. Anterior adductor scar generally of normal length and width, but short in some species and narrow in others; usually parallel to pallial line, but may diverge sharply or curve away gently from it; posterior adductor scar commonly elliptical, sometimes round; anterior pedal retractor scar almost always evident, but posterior one may or may not be. Hinge most commonly has two cardinal teeth in each valve, the right posterior one generally somewhat larger than the right anterior one and slightly bifid; cardinals in left valve closely parallel; single anterior and posterior lateral teeth in right valve fitting into double laterals in left; right anterior cardinal frequently reduced in size or absent; less often, either cardinals or laterals, or both, may be absent or obsolescent. Pallial blood vessel scar present in at least some individuals, usually the larger ones, of each species. Inner ventral margin usually denticulate.

Text-figure 3 summarizes the probable course of evolution within the *Lucina* lineage, whose first undoubted representative, a species of the subgenus *Phacoides,* appears in the Late Cretaceous (Campanian) of the Middle East. *Phacoides,* characterized by an elongate, medium-sized shell with two orders of concentric sculpture, by distinct or conspicuous dorsal areas, and by having strong laterals but weak cardinals, is represented in European Tertiary strata from Eocene through Miocene time and in North America from Paleocene time to the Recent; it is also abundant in the Recent Indo-Pacific fauna.

Most of the Tertiary and Recent species of *Phacoides* have conspicuous dorsal areas, as do species belonging to



Text-figure 3. Probable phylogeny of the *Lucina* lineage. In this and succeeding phylogenetic diagrams, solid lines indicate the known and dashed lines the inferred duration of taxa. Dotted lines indicate alternative interpretations of phylogeny. Note that the space allotted to the various time divisions is not proportional to their actual duration; Mesozoic time, especially, is quite compressed relative to Cenozoic time. To aid in visualization of trends in morphological characters, each subgenus is illustrated by a schematic drawing of the type species or another representative species. Drawings are not all to the same scale; approximate actual lengths are as follows: *Bellucina*, *Callucina?* (= *C. papyracea* group), and *Pleurolucina*, 5 mm; *Cavilinga*, *Parvilucina*, *Parvilucina?*, *Recurvella*, *Luciniola*, and *Lucinisca*, 10 mm; *Callucina* and *Mesolinga*, 15 mm; *Here*, 20 mm; *Lucina*, 30 mm; *Phacoides* and *Stewartia*, 45 mm.

FIGURE 3.

*Lucina s. s.* This group, which is first represented in the middle Eocene Lisbon Formation of Alabama, may have been derived from *Phacoides* by loss of the second-order concentric ribs and by increase in inflation and in dorsoventral elongation. *Lucina s. s.*, recorded from middle Eocene through Recent time in eastern North America and the Caribbean and also represented in the European Oligocene and Miocene, has changed little throughout its history, except that the Eocene species are of small size (length about 12 mm), while those of the late Tertiary and Recent are about 20 to 40 mm long.

*Lucina s. s.* is probably ancestral to two or three other subgenera. One, *Here,* first appears in the late Eocene of Colombia and is like *Lucina s. s.* in nearly all respects except for the presence of a deeply excavated lunule which perforates the hinge plate and partly or completely effaces the cardinal teeth of the right valve. *Here* is recorded from Oligocene time to the Recent on the west coast of southern California and of Mexico. One Miocene species of *Lucina s. s., L. (L.) glenni* (Dall), has a lunule which is deeply excavated in young specimens but which becomes inconspicuous in adults. *Here* may have been derived from a similar earlier species of *Lucina s. s.* in which the lunule remained deeply excavated throughout ontogeny. It is also possible that both *Lucina* and *Here* are descended from the Paleocene-Oligocene subgenus *Herella* which has a deep lunule but has weaker laterals and less prominent dorsal areas than either *Lucina s. s.* or *Here.*

A Miocene to Recent subgenus, *Stewartia,* is similar in musculature to *Lucina s. s.* but is usually less strongly inflated, with less conspicuous dorsal areas, and is edentulous. The striking similarity between the interiors of the shells of the type species, *L. (Stewartia) anodonta* Say and *L. (Lucina) pensylvanica* (Linné) (cf. Plate 28, figure 11, and Plate 25, figure 2), make it appear likely that *Stewartia* was derived from *Lucina s. s.* by loss of the hinge teeth and reduction in inflation. Probably closely related to *Stewartia* is *Lepilucina,* from the Miocene of Ecuador. Its dentition and dorsal areas are like those of *Lucina s. s.,* and the musculature is like that of *Lucina s. s.* and *Stewartia.* The concentric ribs are elevated, giving the shell a rugose surface.

*Phacoides* may be ancestral to the Eocene subgenus *Plastomiltha* which has conspicuous dorsal areas, two orders of concentric sculpture, and a long, narrow anterior adductor. In these respects it resembles *Phacoides;* in *Plastomiltha* the cardinal teeth are strong and laterals are lacking. Conversely, *Phacoides* has well-developed laterals and weak or obsolescent cardinals; *Lucina s. s.* and *Here* also show a tendency toward reduction of the cardinals, with the laterals remaining strong. The combination of strong cardinals, no laterals, and an unusually long anterior adductor also occurs in *Miltha s. s.* For this reason *Plastomiltha* and other subgenera considered related to it have been placed in the *Miltha* lineage; this problem is further discussed in the section on that lineage.

First appearing in Paleocene time is a group of very small (length less than 10 mm) species with extremely short, curved anterior adductors and with concentric sculpture. Species of this group may have well-developed laterals, rudimentary ones, or none. For example, the early Eocene *Lucina sabelli* Gardner, from Texas, has lateral dentition, whereas laterals in a contemporaneous Alabama species, *L. ulrichi* Harris, are absent or weak. Chavan (1937) placed those species of this group having laterals in *Parvilucina* and those lacking laterals in *Callucina.* Dall (1901b) defined these subgenera not only on differences in dentition, but also on differences in sculpture (radials well developed in *Parvilucina,* generally present only in the umbonal region in *Callucina*) and in length and shape of the anterior adductor (short and curved in *Parvilucina;* of normal length and straight in *Callucina*). The correlation between dentition and musculature does not hold in the Eocene species; and the characteristic patterns of sculpture are first seen in Miocene time. It seems likely that both *Callucina* and *Parvilucina* are descended from a small early Tertiary species with a short anterior adductor and normal dentition (see Text-figure 9). Because of the rarity of Oligocene lucinid species, it is difficult to determine whether such Eocene species as *L. (Callucina) papyracea* Lea are directly ancestral to the Miocene to Recent species which lack laterals and have the typical *Callucina* musculature and sculpture. In North America, the only known Oligocene species belonging to the *Callucina-Parvilucina* group is *L. choctavensis* Meyer, which does have laterals. Also arguing against basing the *Callucina-Parvilucina* dichotomy on the presence or absence of lateral dentition alone is the existence of *L. actinoides* (Maury), which is contemporaneous (middle Miocene of Florida) with the earliest undoubted North American species of *Callucina, L. (C.) pauperata* Guppy, from Jamaica. The two species are alike in sculpture and musculature, but *L. actinoides* has lateral teeth, whereas *L. (C.) pauperata* does not (see Text-figure 9). Chavan (1959b, 1961) proposed two new subgenera of *Callucina,* one with a European Eocene type species and the other with a Recent Australian type, as well as a new European Eocene subgenus of *Parvilucina.* Because all these groups were outside the geographic scope of the phenetic study, I have not attempted to determine whether some of the species discussed here should be transferred to the new subgenera.

Possibly also derived from the ancestral *Callucina-Parvilucina* line in Paleocene or early Eocene time is *Cavilinga.* This subgenus is known from middle Eocene through Recent time. Its Eocene representatives resemble species such as *L. (Parvilucina?) sabelli* (Gardner) in their very small size, strong cardinal and lateral teeth, strong inflation, concentric sculpture, and faint dorsal areas. *Cavilinga,* however, has a normally long anterior adductor, curved away from the pallial line. Species of *Cavilinga* are variable in shape (particularly in height/length and anterior length/total length ratios) and in the number and the regularity of spacing of growth rings. In the Miocene species, strong anteroposterior elongation and lack of growth rings are characteristic of forms at the northern part of the distribution of the species, whereas strong dorsoventral elongation and deep, regularly spaced growth rings characterize southerly individuals. In Eocene specimens from a single locality, both extremes as well as intermediate forms are found. Two species which Chavan (1937) placed in *Callucina, L. lampra* (Dall) and *L. lingualis* Carpenter, are probably the Recent West Coast analogues of the Miocene to Recent type species of *Cavilinga, L. (C.) trisulcata* Conrad, from the southeastern United States and the Caribbean.

A problematic group, represented by only three middle and upper Eocene species, is *Recurvella.* It has strongly curved beaks whose elevation is accentuated by the absence of a lunule. The very small size, short anterior adductor, and absence of laterals indicate that *Recurvella* may have branched off the *Callucina-Parvilucina* line in Eocene time. The conspicuous dorsal areas may indicate a closer relationship to *Lucina s. s.,* in which the lunule is generally inconspicuous except in juveniles. Just as *Here* seems to have been derived from *Lucina s. s.* by increasing the depth of the lunule, *Recurvella* may have evolved from it by losing the same structure. *Recurvella* appears to have become extinct rapidly, not giving rise to any other lucinid group.

Three subgenera of *Lucina* are first recorded, at least in North America, in Miocene time. All are characterized by distinctive types of radial sculpture. In *Lucinisca,* the sculpture is generally coarse, and the concentric ribbing varies from slightly stronger than the radials to almost completely absent. Like the radially sculptured Miocene to Recent species of *Parvilucina, Lucinisca* has about 20 thin radials. Most species of *Bellucina* have about 10 radial ribs which are broader and flatter than those of *Lucinisca;* an example is *L. (Bellucina) amiantus* (Dall). The type species, *L. (B.) semperiana* Issel, however, has more numerous, narrower radials which give the shell a cancellate surface like that of *Parvilucina.* A middle Miocene species, *L. (B.) actina* (Dall), which may represent a transition between *Parvilucina* and *Bellucina,* more closely resembles *semperiana* in sculpture than it does *amiantus. Pleurolucina,* also of Miocene origin, has four broad radial ribs, all of equal size. Some species probably related to *Pleurolucina* [*e. g. L. (P.?) leucocymoides* (Lowe)] have one narrow anterior radial rib and one broad central one. *Lucinisca, Bellucina,* and *Pleurolucina* all have well-developed laterals, a single right cardinal or two right cardinals the anterior one of which is reduced, an anterior adductor of normal length and width, and distinct or conspicuous dorsal areas. A fourth group of species with cancellate sculpture like that of *Parvilucina* — *Lucina costata* d'Orbigny is an example — has generally been referred to *Ctena,* but the strong inflation, distinct dorsal areas (intermediate in strength between those of *Parvilucina* and those of *Lucinisca*), denticulate inner ventral margin, and moderate anterior expansion indicate that these species belong to the *Lucina* lineage. The musculature and dentition are like those of *Lucinisca* and *Bellucina.* It seems likely that this group is related to the *Callucina-Parvilucina* group (Text-fig. 9). Like *Lucinisca, Bellucina,* and *Pleurolucina,* the *L. costata* group is first known in Miocene time. It may eventually merit separate subgeneric status. Pending study of Chavan's new subgenera of *Parvilucina* and *Callucina,* I have provisionally referred it to *Parvilucina.*

It is tempting to regard *Parvilucina?, Lucinisca, Bellucina,* and *Pleurolucina* as forming a phyletic progression wth sequential decrease in number and increase in size of the radial ribs. Such an interpretation, however, seems negated by the fact that all appear in the fossil record in early Miocene strata. Too, there is some evidence that *Pleurolucina* is most closely related to *Lucina s. s.* Species of *Pleurolucina* have a "figure-8"-shaped lunule like that of *L. (L.) pensylvanica.* Paralleling the situation in *Lucina s. s.* and *Here,* the lunule is shallow in some species of *Pleurolucina* and deeply excavated in others [which Olsson and Harbison (1953) have distinguished as *Dallucina*]. The species herein placed in *Pleurolucina* which have only two radial ribs have been referred by some authors to *Lucina s. s.* or *Here,* depending on the depth of the lunule. They, too, date from Miocene time, and it is possible that the evolution of the radial ribbing in *Pleurolucina* occurred by increase rather than by decrease in the number of ribs.

*Parvilucina*? (= *L. costata* group), *Lucinisca*, and *Bellucina* may indeed be closely related, particularly since juveniles of species of the first two are difficult to distinguish from each other and from adults of the smaller *Bellucina*. They are probably also related to *L. (Callucina) radians* Conrad and *L. (Parvilucina) tenuisculpta* Carpenter. It seems likely that in Oligocene and early Miocene time the *Lucina* lineage experienced a small evolutionary radiation with the development of several combinations of dentition, musculature, and surface sculpture. Some of the subgenera involved in this radiation may have existed earlier in the Tertiary — Chavan (1937) noted one middle Eocene species, *Lucina (Parvilucina) ligata* (Cossmann and Pissarro) which may belong to *Parvilucina* or *Bellucina* — not becoming abundant until later. The Miocene radiation of the Lucinidae is paralleled in many other molluscan groups (Stewart, 1930).

It is possible to regard the *Lucina* lineage as containing two major groups of subgenera. One, composed of *Phacoides*, *Lucina s. s.*, *Here*, *Stewartia*, and possibly *Recurvella* and *Pleurolucina*, may be derived from the Late Cretaceous *L. (Phacoides) blanckenhorni* Chavan or a similar species. The other, including *Callucina*, *Parvilucina*, *Cavilinga*, *Bellucina*, *Lucinisca*, and *Parvilucina*?, with *Recurvella* and/or *Pleurolucina* doubtfully included, may be derived from a Paleocene species such as *Lucina notata* Deshayes, which Chavan (1937) included in *Parvilucina*. These two groups of subgenera may eventually receive separate generic status, but because they share a common plan of dentition and musculature and because several subgenera could be placed in either group, it appears simplest to consider the members of both as belonging to *Lucina*. The ancestors of both may be descended from species of the European Late Jurassic (Kimmeridgian) *Mesolinga*. The type species, *M. typica* Chavan, is of small size, subround, moderately to strongly inflated, with concentric sculpture (larger specimens sometimes having fine striae between pairs of concentric ribs), an external ligament, well-developed anteror and posterior laterals, two cardinals in each valve, with the right anterior one being partly effaced by the deep, short lunule, and a smooth inner ventral margin. The anterior adductor scar is of normal length and width and closely parallel to the pallial line. Chavan (1952b) compared *Mesolinga* to both *Lucina s. s.* and *Callucina*. Possibly the earliest species of *Lucina s. s.* are in fact direct descendants of *Mesolinga*, and the several unusual features of *Phacoides* indicate that it is a side branch of the *Lucina* lineage not directly ancestral to *Lucina s. s.* and *Here*. Chavan (1952b, p. 90) pointed out that in the absence of intermediate forms such comparisons should be made circumspectly, saying that "it would be fallacious to set them up as established and to try, as unfortunately so many authors do, to find at all costs the ancestors of the many well-known Tertiary genera. Our knowledge — still very fragmentary — of the Mesozoic lucinids implies the existence of branches which were already well differentiated, whose links to the more Recent types are far from being apparent, and whose common origin has yet to be shown" (my translation).

Chavan (1952b) also compared *Mesolinga* to *Luciniola* Skeat and Madsen, whose type is an Early Jurassic species from Germany, *Venus pumila* Goldfuss. This species is similar in size and dentition to *Mesolinga typica*, and has concentric sculpture; the anterior adductor appears to be shorter than in *M. typica*. It is probable that this species is indeed ancestral to *Mesolinga*, and it may even be that *Mesolinga* is ancestral to the *Lucina s. s.* group and *Luciniola* to the *Callucina* group.

Both the Jurassic genera discussed above have faintly marked dorsal areas; but there is a Devonian genus, *Phenacocyclas* LaRocque, in which the internal molds show a strong posterior notch like that at the termination of the conspicuous posterior dorsal area of *Lucina s. s.* The dentition of the type species, *P. pohli* LaRocque, is unknown except for a possible anterior lateral. The anterior adductor scar is straight or slightly curved and of about the same relative length and width as that of *Lucina s. s.* It diverges from the pallial line, and between the pallial line and the anterior adductor, extending to about the midpoint of the shell, there is a roughened area made up of a number of plications which are small where they parallel the adductor, but increase rapidly in size as the plicated area curves around and beyond its ventral tip. Combining this region with the adductor scar gives an extremely elongate differentiated area whose curvature approximately parallels that of the pallial line, closely similar in size and shape to the anterior adductor scar of the Silurian *Ilionia* Billings. McAlester (1965), pointing out the similarity between *Babinka* and *Ilionia*, hypothesized that the elongation of the anterior adductor scar in the lucinoids resulted from a fusion of the radially elongate anterior adductor of *Babinka* with a ventrally elongate impression thought to represent a specialized ciliary sorting area. Possibly such a modification of the mantle produced the plicated anterior region of *Phenacocyclas*. This genus may represent a little-modified descendant of a form intermediate between *Babinka* and *Ilionia*. Or it may be that in the earliest lucinids there was a rapid expansion of the ciliary sorting area and incorporation of it into the anterior adductor. Subsequent increase in the efficiency of the cilia on the epithelium of the anterior adductor may have permitted the reduction in size of the muscle. The sorting area may have been retained as an adjunct sorting mechanism, being lost eventually as the mechanisms of the gills and adductor became more efficient.

Another possible early member of the *Lucina* lineage is *Crassatellopsis* Beushausen, from the European Devonian. Its dentition (large cardinals, no laterals) and the size and shape of the shell are reminiscent of the Eocene *Recurvella.* The anterior adductor scar is slightly elongate. It may, however, not be a lucinid, but perhaps is an early member of the Crassatellacea. Its occurrence lends support from the fossil record to Allen's (1968) suggestion that the Lucinacea and the Crassatellacea are closely related.

### THE CODAKIA LINEAGE

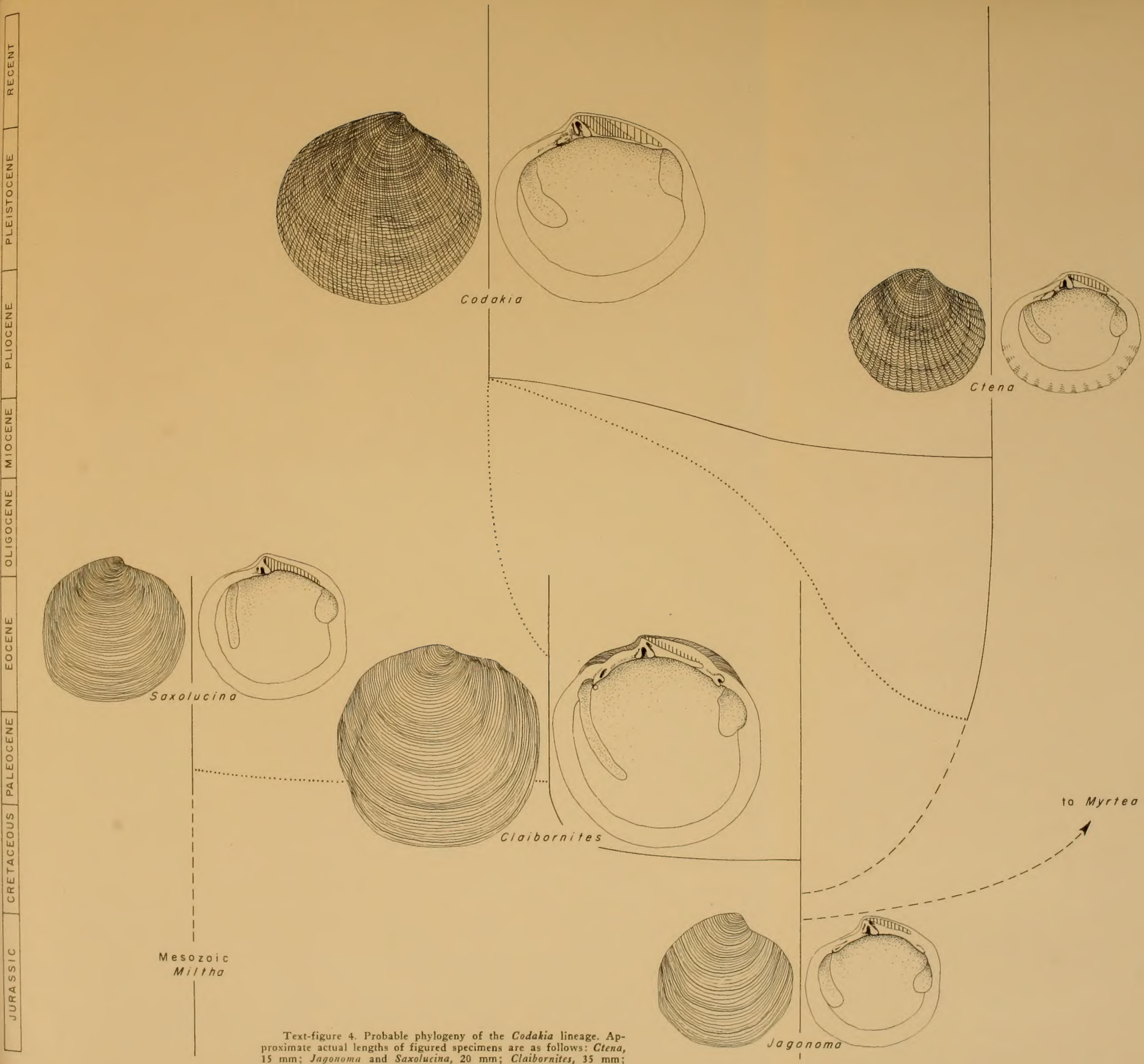
More homogeneous in sculpture, shape, and dentition than the *Lucina* lineage, this genus includes species with an external ligament and others whose ligament is deeply inset, and has a wider range of sizes among its constituent species than does *Lucina.* A number of generic names have been proposed for distinctive species or species groups of this lineage, but most appear to be synonyms of *Codakia s. s.* Most are based on species from the Indo-Pacific, where the group is most diverse. Only two subgenera included in the phenetic study, *Codakia s. s.* and *Ctena,* definitely belong to this lineage; a third, *Claibornites,* is referred tentatively to it. Text-figure 4 presents the probable course of evolution of the *Codakia* lineage.

*Diagnosis of the genus Codakia.* — Shell of small to very large size, longer than high, flat to moderately inflated, anterior expansion small (in adults of *Codakia*) or moderate to great (in *Ctena* and in juveniles of *Codakia*). Sculpture generally both radial and concentric, with radial sculpture dominant, radial ribs occasionally (*Codakia s. s.*) or frequently (*Ctena*) bifurcate; radials may be faint or absent; growth rings usually irregularly spaced. Dorsal areas faint, set off only by slight change in sculpture. No periostracum. Size, shape, and depth of lunule variable; ligament deeply inset (*Codakia s. s.*) or external (*Ctena*). Anterior adductor scar generally of normal length and width and curved away from pallial line, may be straight and variable in width. Posterior adductor scar elliptical; neither pedal retractor, or only anterior one, separate from adductors. Hinge with two cardinals in each valve, right posterior one entire or slightly bifid; anterior and posterior laterals single in right valve, double in left; posterior laterals may be effaced when ligament is deeply inset. Shell interior often pink or yellow in color. Pallial blood vessel scar present. Inner ventral margin smooth.

*"Lucina" parvilineata* Shumard, from the Upper Cretaceous (Maestrichtian) Navarro Group of Texas, is a possible early representative of the subgenus *Ctena.* The interior of this shell is unknown, but the small size (length 15-20 mm), strong anterior expansion, anteroposterior elongation, faint radial sculpture, and faint dorsal areas indicate a relationship to the type species, *Codakia (Ctena) mexicana* Dall. The short, wide, deep lunule is like that of *Codakia s. s.* rather than like the long, oval, shallow lunule of *C. mexicana.* Species definitely placed in *Ctena* range from late Eocene through Miocene time in Europe (Chavan, 1937). The record of *Ctena* in North America resumes — or begins — in early Miocene time and continues to the present. *Ctena* is widely distributed in warm waters.

*Ctena* is probably ancestral to *Codakia s. s.* Chavan (1937) reported one possible member of the latter subgenus from the Paleocene of France, but he stated that *Codakia s. s.* is principally a Miocene to Recent subgenus. One line of evidence for the relationship between *Codakia s. s.* and *Ctena* is the similarity in shape between juveniles of the former and adults of the latter; both have a strong anterior expansion but can be distinguished by differences in the ligament. The anterior end of the shell becomes proportionally smaller with growth in *Codakia.* There is also a small middle Miocene species, strongly anteriorly expanded, which has a deeply inset ligament only partly effacing the posterior laterals, and sculpture similar to that of *C. (Codakia) orbicularis* (Linné), the type species of *Codakia.* The Miocene species, *C. (Codakia?) lomonea* Woodring, is morphologically intermediate between *Codakia s. s.* and *Ctena,* though it appears slightly too late in the record to be a direct link between them. Possibly the numerous Miocene to Recent species of *Codakia s.s.* were derived from an early Miocene species like *C. (C.?) lomonea* rather than from the French Paleocene species. In Text-figure 4 I have thus indicated two different possible times of origin of *Codakia s. s. C. (C.?) lomonea* also resembles the Recent Australian *C. (Epicodakia) gunnamatta* Iredale, which has a deeply inset ligament, like *Codakia s. s.,* but which has sculpture and dentition like those of *Ctena.*

Also, *Codakia s. s.* may be represented by the Upper Cretaceous (Maestrichtian) and Paleocene *Codakia? cedrensis* (Stanton) from North Dakota and South Dakota. Speden (1970) tentatively referred this species to *Epilucina* [in the



Text-figure 4. Probable phylogeny of the *Codakia* lineage. Approximate actual lengths of figured specimens are as follows: *Ctena*, 15 mm; *Jagonoma* and *Saxolucina*, 20 mm; *Claibornites*, 35 mm; *Codakia*, 45 mm.

FIGURE 4.

sense in which Chavan (1937) used this name, as synonymous with the Paleogene subgenus *Claibornites* and as a subgenus of *Codakia*]. *C.*? *cedrensis* has a deeply inset ligament and has both anterior and posterior lateral teeth. It differs from *Codakia s. s.* and *Ctena* in lacking radial sculpture; also, the shell is more rounded than in these subgenera, and the anterior adductor is straight and parallel to the pallial line rather than being curved away from it. The type species of *Claibornites*, *C. symmetrica* (Conrad), also has a rounded shell, lacks radial sculpture, and has both a deeply inset ligament and well-developed anterior and posterior laterals; its straight anterior adductor scar is longer and narrower than that of *cedrensis*.

If *Codakia*? *cedrensis* is the earliest member of *Claibornites* and *Codakia*? *parvilineata* the first *Ctena*, both these subgenera appear as fossils in Upper Cretaceous time, one in the Western Interior and one in the Gulf Coast region. They may have a common ancestor in *Jagonoma*, a Jurassic to Pliocene group with faint radial sculpture overlying concentric ribs of two orders, with an external ligament, and with dentition and musculature like those of *Codakia*? *cedrensis*. Chavan (1946b) considered the Jurassic type species of *Jagonoma*, *Lucina circumcisa* Zittell and Goubert, the precursor of *Ctena*.

The *Codakia* and the *Miltha* lineages may be linked by two groups proposed by Stewart (1930) as subgenera of *Claibornites*: *Saxolucina* (Eocene, France) and *Codalucina* (Paleocene, France). Both have a deeply inset ligament like that of *Claibornites* but differ from this subgenus in lacking lateral teeth and in having a shorter, broader anterior adductor (similar in shape to that of *C.*? *cedrensis*). Chavan (1938) considered *Saxolucina* most closely related to *Plastomiltha*, a probable member of the *Miltha* lineage. Cvancara (1966) pointed out similarities between *C.*? *cedrensis* and both *Plastomiltha* and *Codalucina*. It may be that the pattern of dentition in *Claibornites* was inherited from *Jagonoma*; that *Saxolucina* evolved from an early species of *Claibornites* by loss of the laterals; and that the development of the long, narrow anterior adductor scar in *Claibornites*, similar to that of several subgenera of *Miltha*, occurred independently in *Claibornites* after the branching off of *Saxolucina*. Alternatively, both *Saxolucina* and *Claibornites* may be descended from Mesozoic members of the *Miltha* lineage, with *Saxolucina* having retained the primitive pattern of dentition and developed a shorter anterior adductor, while *Claibornites* evolved lateral dentition and retained the elongate adductor.

### THE MILTHA LINEAGE

The subgenera here included in the *Miltha* lineage, with the exception of *Lucinoma*, were represented in the phenetic study by species which Dall (1901b, 1903) placed in *Miltha*. Dall considered *Miltha* a subgenus of his broadly inclusive genus *Phacoides*, and divided it into three informally designated species groups; all these subgroups have since been formally named. It is possible, however, that the *Miltha* lineage is polyphyletic, since some of its subgenera may be derived from species of the *Lucina* lineage and others from Jurassic species which appear to have the characteristic features of the *Miltha* lineage. Text-figure 5 and Text-figure 6 thus indicate two alternative interpretations of the phylogeny of the subgenera here grouped as the *Miltha* lineage.

*Diagnosis of the genus Miltha.* — Shell of medium to very large size, higher than long to longer than high, flat to moderately inflated, anterior expansion moderate to great. Surface sculpture fine to rugose; concentrics either all of equal prominence, with irregularly spaced growth rings, or composed of two orders of concentrics; radials, when present, faint. Dorsal areas faint to conspicuous. Periostracum thin or absent except in cold-water species. Lunule generally triangular, deep, slightly asymmetrical, variable in length and width. Ligament external or deeply inset; position of ligament may vary within a species. Anterior adductor generally very long, varying in width from narrow to wide, straight or curved; posterior adductor scar elliptical; anterior pedal retractor scar generally separate from adductor, posterior one partly separate, above or on inner side of adductor. Hinge plate usually wide; no laterals; two strong cardinals in each valve; right posterior cardinal slightly to strongly bifid. Pallial blood vessel scar present. Inner ventral margin smooth.

Three of the subgenera of *Miltha* originate in Paleocene or early Eocene time. *Eomiltha* is elongated anteroposteriorly, with a curved, unusually long anterior adductor and strong cardinal teeth, the right posterior and left anterior ones being so strongly bifid that there appear to be three cardinals in each valve. The ligament is short, triangular, and deeply inset; the ligament, curvature of the anterior adductor, and anteroposterior elongation recall *Codakia s. s.* *Eomiltha* is primarily a Paleocene and Eocene subgenus, but there are at least one middle Miocene and one Recent representative. The type species is of medium size, but the largest lucinid known, *Lucina megameris* Dall, from the late Eocene of Jamaica and Florida, may be an *Eomiltha*. This species, which attains a length of about 250 mm, has an extremely long, curved anterior adductor; the dentition is unknown.

*Miltha s. s.* is questionably recorded from the Paleocene of Texas and of California and from the middle Eocene of Mexico. The earliest species confidently assigned to the subgenus, however, are late Eocene in age. *Miltha s. s.* is also known in the Oligocene and is fairly common in the Miocene, but only two rare Recent species are known. This subgenus is characterized by shells of large size, higher than long, with conspicuous dorsal areas and an unusually long and wide anterior adductor; the ligament is external or only slightly inset, and the right posterior cardinal is not strongly bifid. *Miltha s. s.* is the only inequivalve lucinid (though not all its species are inequivalve). Chavan (1938) considered *Miltha s. s.* to be derived from *Recticardo,* a principally Paleocene European group, smaller in size and more rounded than *Miltha s. s.* and with an anterior adductor of normal length and width. Chavan also believed *Miltha s. s.* to be closely related to *Saxolucina,* discussed above in connection with the *Codakia* lineage, and considered *Recticardo* a link between *Eomiltha* and *Miltha s. s.* It is possible that a species such as *Codakia? (Claibornites?) cedrensis* gave rise, late in Cretaceous time, to *Saxolucina* and also to *Recticardo* and thence to *Miltha s. s.* and *Eomiltha;* however, there is evidence for a more remote common ancestry of at least the last three subgenera.

*Plastomiltha,* proposed by Stewart (1930) as a subgenus of *Miltha,* was considered by Chavan (1938) to have been derived from *Saxolucina* in Paleocene time. *Saxolucina* and *Plastomiltha* are alike, but *Plastomiltha* has stronger dorsal areas than *Saxolucina* and has two orders of concentric sculpture. In both these respects, as well as in the narrow, moderately to strongly elongate anterior adductor, *Plastomiltha* resembles *Phacoides.* It is possible that these two taxa had a common ancestor with cardinals and laterals about equally strong, and that the lateral dentition became prominent and the cardinals effaced in *Phacoides,* with the converse process occurring in *Plastomiltha.* In this case *Plastomiltha* and its descendants would have to be referred to the *Lucina* rather than the *Miltha* lineage. Kinship of *Plastomiltha* with the *Miltha* lineage is an equally plausible postulate because *Miltha s. s.* also has a strongly elongate anterior adductor and conspicuous dorsal areas. Concentric sculpture of two orders has evidently also developed independently in another lucinid lineage, *Myrtea.* The combination of strong cardinals, a long anterior adductor, and no laterals may have evolved as one solution to the problem of keeping the valves interlocked, correctly aligned, and tightly closed. A more normal anterior adductor with cardinals and laterals of about equal strength, or elongation of the anterior adductor combined with reduction of the cardinals and increase in strength of the laterals, may be equally viable alternatives. Similarly, in the evolution of *Lucina (Callucina),* the loss of laterals has evidently accompanied increase in the relative length of the anterior adductor.

*Plastomiltha,* known only from the Eocene strata of the Mississippi Embayment, appears to have given rise to two other subgenera. *Lucinoma* is characteristic of cold waters, the several Recent species being found either at high latitudes or in deep water. Recorded from Miocene time onward, it differs from *Plastomiltha* in its great anteroposterior elongation, less conspicuous dorsal areas, and often deeply inset ligament but is similar to it in dentition and sculpture.

*Armimiltha,* which is represented from late Oligocene through Pliocene time in Florida, is elongated dorsoventrally and has rugose surface sculpture with fine concentric striae between strongly raised ribs. The narrow anterior adductor scar, consisting of a long ventral portion diverging sharply from a short dorsal portion, appears to have been derived from that of *Plastomiltha* by fusion of the dorsal part of the adductor with the anterior pedal retractor scar. The posterior pedal retractor of *Armimiltha* forms a bulge on the inside of the posterior adductor; the posterior pedal retractor in *Plastomiltha* is slightly offset toward the inside of the adductor, rather than being situated directly above it.

Two genera with Late Jurassic type species, *Mesomiltha* and *Discomiltha,* may be ancestral to some or all of the Cenozoic genera of the *Miltha* lineage. In both the cardinal teeth are present and the laterals absent or weak. According to Chavan (1938, 1952b), in species of *Mesomiltha* the prominence of the lateral dentition, particularly of the posterior laterals, may vary within a species; the posterior laterals may or may not be present. *Mesomiltha* is not completely satisfactory as a potential ancestor of the entire *Miltha* lineage because of its small size (length about 10 mm), faintly indicated or missing right anterior cardinal, and anterior adductor scar of normal dimensions; it is, however, similar to *Recticardo* (Chavan, 1938). Chavan originally considered *Mesomiltha* to include several species, nearly all European and ranging in age from Early Jurassic through Pliocene, which also seemed similar to *Eomiltha.* He since placed some of the species originally included in *Mesomiltha* in other genus-group taxa (Chavan, 1952b) and gave its range as Lower Jurassic to Upper Jurassic, with questionable representation in the Cretaceous (Chavan, 1969).

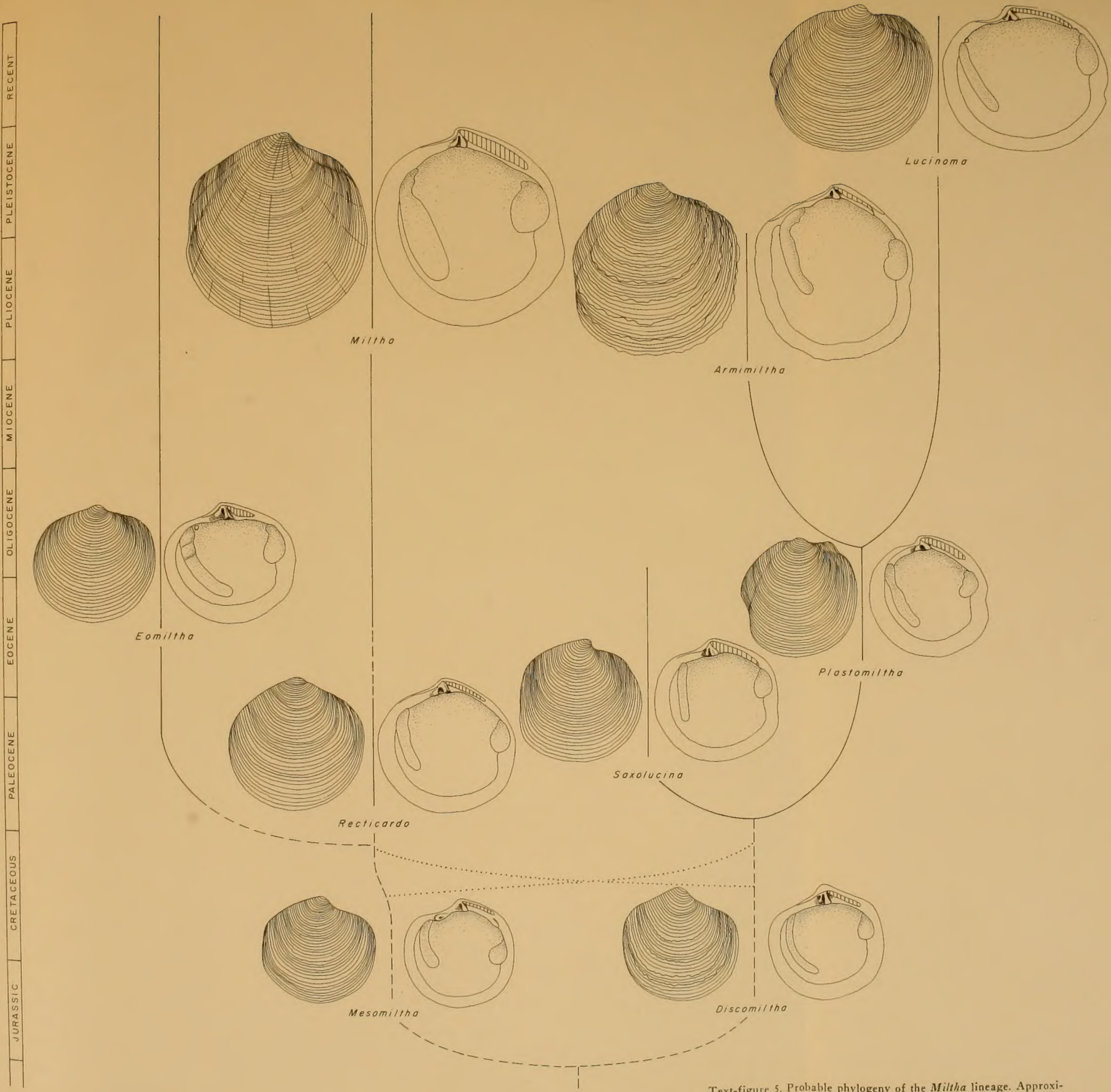
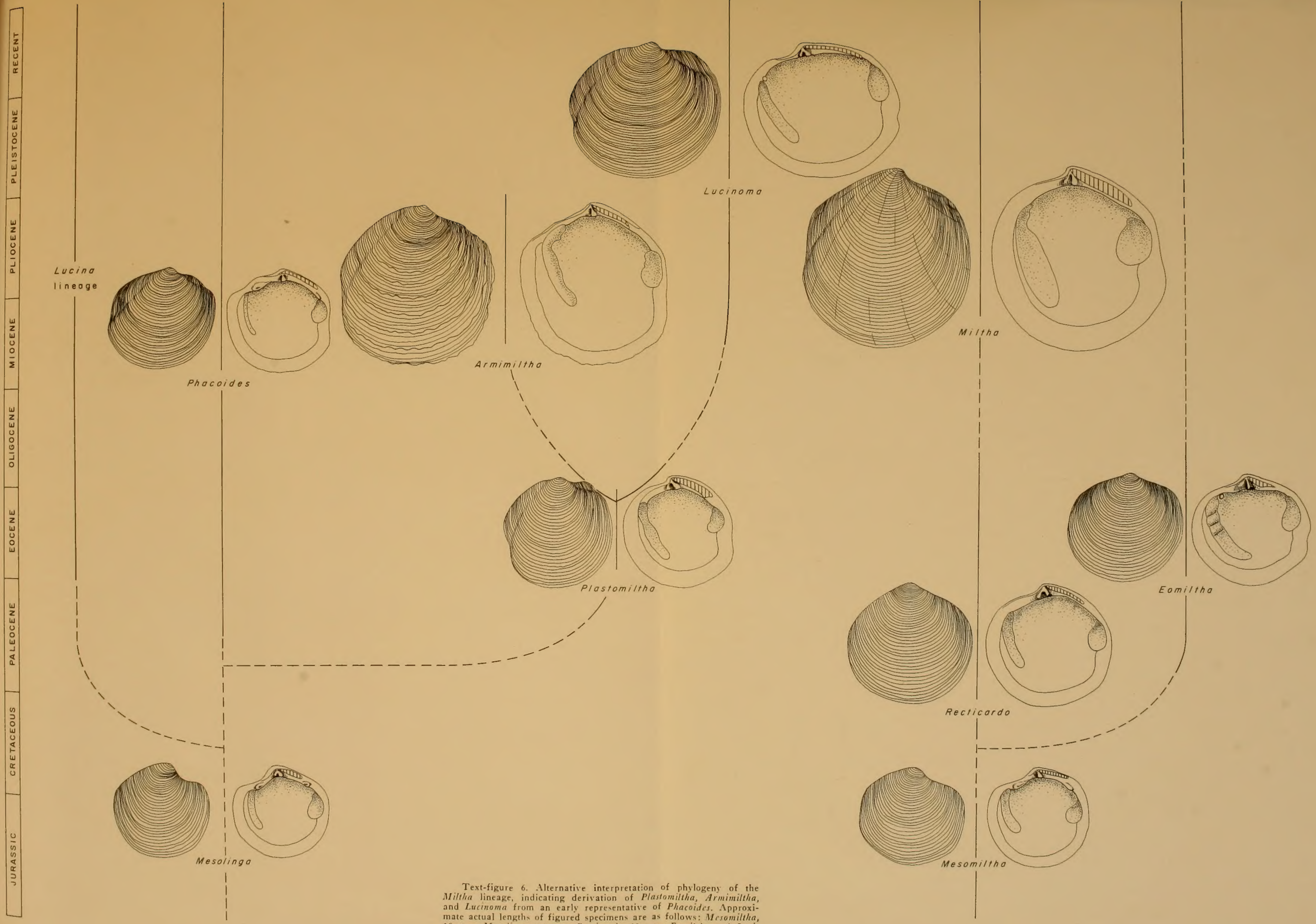


FIGURE 5.

Text-figure 5. Probable phylogeny of the *Miltha* lineage. Approximate actual lengths of figured specimens are as follows: *Mesomiltha*, 10 mm; *Recticardo* and *Saxolucina*, 20 mm; *Discomiltha*, 30 mm; *Eomiltha* and *Lucinoma*, 35 mm; *Plastomiltha*, 40 mm; *Armimiltha* and *Miltha*, 60 mm.



Text-figure 6. Alternative interpretation of phylogeny of the *Miltha* lineage, indicating derivation of *Plastomiltha*, *Armimiltha*, and *Lucinoma* from an early representative of *Phacoides*. Approximate actual lengths of figured specimens are as follows: *Mesomiltha*, 10 mm; *Mesolinga*, 15 mm; *Recticardo*, 20 mm; *Eomiltha* and *Lucinoma*, 35 mm; *Plastomiltha*, 40 mm; *Phacoides*, 45 mm; *Armimiltha* and *Miltha*, 60 mm.

FIGURE 6.

Chavan (1938) originally included the type species of *Discomiltha, D. oehlerti,* in *Saxolucina.* Comparable in size to *Saxolucina* and *Plastomiltha* (length and height about 30 mm), and with a long, narrow, somewhat curved anterior adductor, a partly inset ligament, and a tendency toward development of two orders of concentric sculpture, it may be ancestral to these two subgenera and their descendants. As it could also have given rise to either *Miltha s.s.* or *Eomiltha,* or both, there seems to be no compelling evidence for placing these subgenera in a different lineage than *Plastomiltha.* From a viewpoint considering the degree of diversity evident in Mesozoic lucinids, it appears reasonable to treat *Mesomiltha* and *Discomiltha* as different subgenera of a single genus, so that even if the separation between *Miltha s. s.-Eomiltha* and *Plastomiltha* dates back as far as Late Jurassic time, the *Miltha* lineage remains monophyletic at the generic level. An analogous situation exists in the *Lucina* lineage.

Two Paleozoic taxa may be early members of the *Miltha* lineage. The Silurian *Ilionia* is strikingly similar in its anteroposterior elongation and its extremely long, curved anterior adductor scar to *Eomiltha.* Because the dentition and sculpture of *Ilionia* are unknown (generally only internal molds are preserved), the resemblance may be only superficial. *Paracyclas,* the second possible member of the *Miltha* lineage, is the most abundant and diverse Paleozoic lucinid, being represented by a number of species in Silurian and Devonian rocks of North America and Europe. Species of *Paracyclas* are generally preserved as composite molds (McAlester, 1962) which show fine concentric sculpture. The shell is often much deformed by post-depositional processes, but the original shape appears to have been approximately round and strongly inflated. Specimens showing both internal and external shell characters are rare. McAlester (1963) figured a species questionably assigned to *Paracyclas* which has a slightly curved anterior adductor scar of normal length and width, but a species of *Paracyclas* figured by LaRocque (1950) has a narrower anterior adductor. Considering the difficulty of associating interior with exterior features in *Paracyclas,* attempts to relate it to Mesozoic and Cenozoic forms must be even more speculative. It is possible, in fact, that *Paracyclas* does not belong to the Lucinidae. Chavan (1959a) assigned it to the Mactromyidae, a small group of probable lucinoid affinity. McAlester (1965), on the basis of its strong inflation and rounded form, suggested that it might be an early member of the Ungulinidae. Possibly the ancestors of more than one lucinoid taxon will be found among the diverse species of *Paracyclas.*

### THE MYRTEA LINEAGE

This group is characteristic of cold waters; its Recent representatives are found at great depths or at high latitudes, and some of its fossil occurrences are also interpreted as indicating a cold-water habitat. Text-figure 7 shows the probable phylogeny of the *Myrtea* lineage.

*Diagnosis of the genus Myrtea.* — Shell of very small to medium size, moderately inflated, anterior expansion generally moderate. Surface sculpture dominantly concentric, ribs evenly spaced, sometimes with fine second-order concentrics, or short, discontinuous radials, between concentrics; growth rings, when present, irregularly spaced. Concentric ribs often reflected into spines at posterior dorsal margin; dorsal areas faint. Lunule generally long, triangular or oval. Ligament external. Anterior adductor scar of normal length and width, straight or curved, usually diverging from pallial line; posterior adductor scar round or elliptical. Anterior pedal retractor scar separate from adductor, posterior one partly separate or not evident. Hinge plate narrow, with anterior and posterior laterals single in right valve, double in left; one or two cardinals in right valve, two in left; laterals, or all teeth, may be obsolescent or absent. Pallial blood vessel scar present or absent. Inner ventral margin usually smooth.

The subgenus *Myrtea s. s.* is probably first represented in North America by species from the Late Cretaceous (Maestrichtian) Navarro Group and early Paleocene Kincaid Formation of Texas. The sculpture, shape, and musculature of these taxa are similar to those of *Myrtea s. s.* The subgenus may also be represented in the middle Eocene of Alabama. The earliest species definitely assignable to *Myrtea s. s.* is the middle Oligocene *M. (M.) vicksburgensis* (Casey) from Mississippi. The Miocene record and Pliocene record of *Myrtea s. s.* are principally European. The type species, *M. (M.) spinifera* (Montagu), is Recent and European. There is one Recent North American species. *Myrtea s. s.* is also known from Australia and Asia.

Dall (1901b) proposed the name *Eulopia* for lucinids closely resembling *Myrtea s. s.* but smaller and having discontinuous radial lines between pairs of concentrics. He included in *Eulopia* three North American-Caribbean species — two Miocene species and the Recent type, *M. (E.) sagrinata* (Dall). Some species of the Recent Australian genus *Notomyrtea* have similar sculpture; it is thus possible that *Eulopia* is not a monophyletic group. The rarity of representatives of *Eulopia* and the patchy fossil record of the group — both probably a consequence of its deep-water habitat — make a decision on its status difficult. Vermicular sculpture similar to that of *Eulopia* also characterizes some Eocene species of the *Anodontia* lineage, providing one of the lines of evidence for considering the *Anodontia* and the *Myrtea* lineages closely related.

Loss of the entire dentition, paralleling similar trends in the *Lucina* and the *Miltha* lineages, may have given rise to the group of species which was represented in the phenetic study by the New England species *Myrtea lens* (Verrill and Smith). Two subgeneric names have been proposed for edentulous species considered to be closely related to *Myrtea: Myrteopsis* was described by Sacco (1901) from the Pliocene of Italy, and the type species of *Levimyrtaea* is from the late Miocene or early Pliocene of Ecuador, from a mudstone which is interpreted as a deep-water deposit (Olsson, 1964). *Myrteopsis* and *Levimyrtaea* are probably synonymous — this synonymy is not unequivocally established, because there is some doubt as to the identity of Sacco's type species — and thus I have tentatively placed *M. lens* in *Myrteopsis*.

The subgenus *Epilucina* is probably a member of the *Myrtea* lineage. Dall (1901b) proposed it as a section of *Callucina*. Chavan (1937, 1969) placed it in *Codakia*, but I have shown in the systematics section that he apparently confused the type species of *Epilucina* with that of *Claibornites*. *E. californica* (Conrad), the type of *Epilucina*, is strikingly similar in shape and sculpture to *M. spinifera* (Montagu); differences in the dentition, musculature, and lunule indicate, however, that the relationship may be distant. The latitudinal distribution of *E. californica* is unusual. The species is common in intertidal areas along the entire coast of California and that of northern Baja California; its distribution thus overlaps both that of the primarily northern species *Lucina (Parvilucina) tenuisculpta* Carpenter and *Miltha (Lucinoma) annulata* (Reeve), and that of numerous Panamic lucinids which range as far north as Baja California or Los Angeles.

*Epilucina californica* may be descended from an Eocene species from Oregon, *Myrtea (Myrtucina) roseburgensis* (Hendon). This species, the type of the subgenus *Myrtucina* Vokes, 1939, is like *E. californica* in shape, configuration of the lunule, and sculpture; its dentition is like that of *M. spinifera*. Unfortunately, the musculature of *M. roseburgensis* is unknown (for this reason the species was omitted from the phenetic study), and no forms have been noted which bridge the stratigraphic gap between the Pliocene-Recent *E. californica* and the Eocene *M. roseburgensis*. The latter species is also similar to *Nymphalucina occidentalis* (Morton). *N. occidentalis*, abundant in the Late Cretaceous (Maestrichtian) of the Western Interior, is about the same size as *M. roseburgensis* and is similar in shape to *M. roseburgensis* and *E. californica*. The presence of two right-valve cardinals and a pallial blood vessel scar indicate similarity to *Epilucina;* the musculature and the symmetrical lunule are like those of *Myrtea s. s.* Some specimens, like *M. spinifera*, have two orders of concentric ribs; others, resembling *E. californica* in this respect, do not. Posterodorsal spines are present on small individuals.

Dall (1901b) considered the single right-valve cardinal in *Myrtea s. s.* and *Eulopia* to be "normal", in contrast to species of other lineages whose loss or reduction of the right anterior cardinal he regarded as a result of the deepening of the lunule, the cardinal tooth not being allowed room to develop. The reduction of the lateral teeth in some species of *Myrtea s. s.* and the loss of the entire dentition in *Myrteopsis*? indicate, however, that the amount of potential variability in the dentition of the *Myrtea* lineage is equivalent to that in other lineages. The *Myrtea* lineage may well comprise two groups of subgenera; one, including *Nymphalucina, Myrtucina,* and *Epilucina,* may have been confined to the temperate waters of the western United States; the other, including *Myrtea s. s., Eulopia,* and *Myrteopsis*?, evidently had some warm-water representatives in Miocene time (species of *Myrtea* and *Eulopia* occur in the Bowden Formation of Jamaica), but its subsequent wider range may have been permitted by adaptation to colder waters. The morphological features characteristic of early members of the two groups may have persisted since their separation. The small Cretaceous, Paleocene, and Eocene species questionably assigned to *Myrtea s. s.* may link the two groups [cf. Speden (1970)]. It is also possible that the *Epilucina* and *Myrtea s. s.* groups have evolved separately since Jurassic or Cretaceous time. Speden (1970) compared *Nymphalucina* to *Jagonoma,* the Jurassic to Pliocene group which Chavan (1946b) considered to include the ancestors of *Ctena. Jagonoma,* which includes some individuals with both two orders of concentric ribs and faint radials, has well-developed laterals and two cardinals in each valve. Both the Cretaceous to Eocene species provisionally included in *Myrtea s.s.,* and *Nymphalucina* and its descendants, could have been derived independently from species of *Jagonoma.* In this case, either or both of the subgroups of the *Myrtea* lineage may have its closest affinities with early species of *Ctena.* The morphological and ecological distinctiveness of *Myrtea s. s., Eulopia, Myrteopsis*?, and *Epilucina,* favor their placement in a distinct genus.

### THE ANODONTIA LINEAGE

This group, characterized by strongly inflated shells and great reduction or complete loss of the dentition, is the youngest of the lucinid lineages. It probably diverged from the *Myrtea* lineage in Paleocene time (Text-figure 7). Text-figure 8 shows another interpretation of the phylogeny of the *Anodontia* lineage indicating a closer relationship to *Loripes* (see below) than to *Myrtea.*

*Diagnosis of the genus Anodontia.* — Shell of very small to very large size, longer than high, strongly inflated, anterior expansion generally small to moderate. Surface sculpture dominantly concentric, sometimes with faint to distinct, discontinuous or continuous radial sculpture; growth rings irregularly spaced. Dorsal areas faint to distinct. Lunule generally shallow, variable in size and shape. Ligament external or slightly inset. Anterior adductor scar of normal length and width, straight, parallel to or diverging from pallial line. Posterior adductor scar elliptical; anterior pedal retractor scar separate from adductor, posterior one not evident. Hinge edentulous or with one cardinal in right valve, two in left, laterals obsolescent or absent. Pallial blood vessel scar present. Inner ventral margin smooth.

Stewart (1930) proposed the subgeneric name *Eophysema* for Eocene species from the Gulf Coast and the Paris Basin. He defined *Eophysema* as having fine to strong radial sculpture and, at least in the juveniles, small cardinal teeth. He considered it to have given rise in Oligocene time to *Anodontia s. s.*, this group being characterized by the absence throughout ontogeny of the hinge teeth. Harris (1946) and Palmer and Brann (1965) showed that there is doubt about the definition of the type species [see discussion of *Anodontia (Eophysema) subvexa* (Conrad) in the systematics section]. Beauchamp (1969) reported representatives of *Eophysema* in the Atlantic Coast Paleocene.

Chavan (1951b) placed the dentate species of *Eophysema* in *Gardnerella,* which he proposed as a subgenus of *Myrtea; M. waltonensis* Gardner, from the middle Miocene of Florida, is the type species. Stewart's premise that the dentition of the various species was modified both throughout the ontogeny of individuals and throughout the time span of the taxon appears reasonable. It is not necessary to assume, as Chavan apparently did, that the same modifications must occur either at the same stage of ontogeny, or at the same time geologically, in all these closely related species. *Gardnerella waltonensis* is probably a descendant of *E. ozarkana* in which the hinge teeth were retained and the radial sculpture partly or completely lost.

In addition to the above-mentioned Eocene and Paleocene species, there is a middle Eocene (Tallahatta Formation, Alabama) species, *Anodontia*? *augustana* Gardner, 1951, which differs from *E. subvexa* in its much larger size (length about 80 mm) and strong anteroposterior elongation; its dentition is unknown. Species undoubtedly belonging to *Anodontia s. s.* are known from Oligocene time to the present; the subgenus is found throughout the world in tropical and subtropical waters. Several generic names which have been proposed are based either on minute differences in sculpture or on differences in geographic distribution. Stewart's (1930) name *Pegophysema* was suggested as a replacement for *Anodontia* because an ambiguous reference in Link's (1807) proposal of the name *Anodontia* made it appear that *Anodontia* referred to the group here called *Phacoides.* The generic name *Loripinus* is based on a Mediterranean species which has an internal ligament and a short, wide anterior adductor (Dall, 1901b). Chavan (1938) believed that Link's *Anodontia alba* belonged to this group, but most other authors have used *A. alba* for a North American and Caribbean species, which Stewart (1930) considered conspecific or at least consubgeneric with the type species of *Pegophysema, Lucina philippiana* Reeve.

The reference of some species to either *Myrtea* or *Eophysema,* the presence of discontinuous radials in some Eocene and Miocene species of the *Anodontia* lineage, the elongate shape, and the occurrence of one right-valve cardinal and obsolescent laterals in some species of *Anodontia* indicate relationship between the *Myrtea* and the *Anodontia* lineages. The *Anodontia* lineage may have diverged early in Tertiary time from the evolutionary line leading to *Myrtea s. s.*, the major changes being a considerable increase in the degree of inflation of the former, increase in its overall size, and loss of the hinge teeth. Chavan (1938) considered *Anodontia* to have been derived from Paleocene representatives of *Monitilora,* a group primarily European in Paleogene time and Indo-Pacific in the Neogene. He believed both *Monitilora* and *Myrtea* to have descended from the Mesozoic *Mesomiltha* which is here considered to have given rise to several Tertiary subgenera of the *Miltha* lineage. Chavan (1969) placed *Mesomiltha* and *Monitilora* in the subfamily Myrteinae and *Anodontia* in the Milthinae. As noted above, I consider it possible that the *Myrtea* and ultimately the *Anodontia* lineages, like the *Codakia* lineage, may descend from Mesozoic representatives of *Jagonoma.*

It is also possible that the *Anodontia* lineage is related to *Loripes* which may be derived from Mesozoic or early Cenozoic members of the *Lucina* lineage or the *Codakia* lineage (see below). Because of this uncertainty about phylogeny and also because of the considerable degree of morphological difference between *Anodontia* and *Myrtea, Anodontia* is here retained as a distinct genus.

### THE LORIPES GROUP

A Recent Mediterranean species included in the phenetic study, *Loripes lacteus* Poli, is the type species of a subgenus belonging to a group which evidently has no fossil record in North America. *L. lacteus* externally resembles small species of *Anodontia,* but it has well-developed dentition and a ligament which is completely internal, not just deeply inset as in *Codakia s. s.* [See Allen (1960).] *Loripes s. s.* is recorded from Miocene to Recent time in Europe. Chavan (1937, 1938) considered *Loripes s. s.* ancestral to the Recent Indo-Pacific subgenera *Pillucina* and *Wallucina.* He found its probable ancestor in *Microloripes,* a Paleocene to Recent, predominantly European taxon which he considered to be derived from the lineage leading to *Codakia s. s.* and *Ctena.* He regarded the internal ligament of *Loripes* and its relatives as the result of continuation of the trend toward internalization seen in *Codakia s. s.* and *Claibornites.*

Another possible phylogenetic interpretation is indicated by Cossmann and Peyrot's (1911) comparison of *Microloripes* to *Parvilucina.* The two taxa are similar in size and dentition. The *Loripes* group may be an offshoot from the small Paleocene and Eocene members of the *Lucina* lineage, or it may be descended from the Mesozoic *Mesolinga.*

Dall (1901b) noted that the large, edentulous species here placed in *Anodontia* had often been referred to *Loripes,* but that members of the former have an external ligament. Dall classified the Mediterranean subgenus *Loripinus* with *Anodontia* because both are edentulous. From his description, the ligament of *Loripinus* is similar to that of *Loripes,* and *Loripinus* has a shorter anterior adductor scar than *Loripes* or *Anodontia.* Like *Loripes, Loripinus* is evidently unrepresented in North America.

I consider it most probable that *Loripes* is related to the *Anodontia* lineage, with *Loripes s. s., Anodontia,* and *Loripinus* having a common ancestry either in *Microloripes* (see Text-figure 8) or in a species of the *Myrtea* lineage (as discussed under *Anodontia*). Because of the lack of North American fossil evidence and because I have not seen specimens of some of the relevant taxa, *Loripes* is here retained as a separate genus.

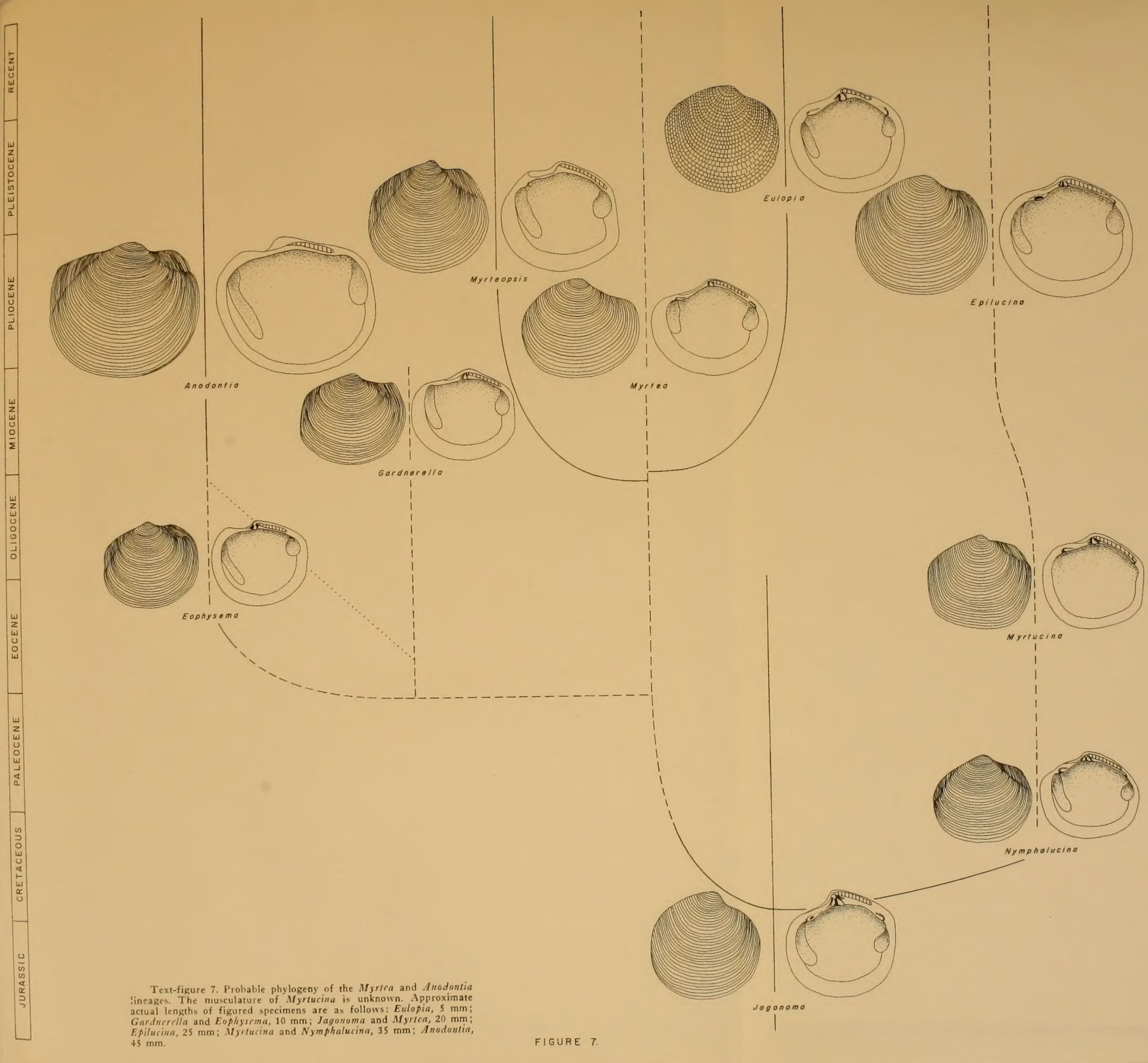
### THE DIVARICELLA GROUP

Chavan (1951a), who divided the species assigned by most workers to the genus *Divaricella* into six genera, was uncertain whether the lucinids with divaricate surface sculpture represented a phylogenetic ensemble whose evolution paralleled that of the other lucinid lineages, or whether each major lucinid group had its divaricate representatives. Most of Chavan's divaricate genera can be analogized with nondivaricate taxa. For example, *Divalinga,* with well-developed cardinals and laterals, a short anterior adductor, an external ligament, and a denticulate inner ventral margin, recalls members of the *Lucina* lineage. *Divalucina,* with obsolescent laterals, well-developed cardinals, a long and narrow anterior adductor, and a smooth inner ventral margin, resembles members of the *Miltha* lineage, such as *Lucinoma* and *Plastomiltha.*

This study includes only three divaricate species, representing two of the genera recognized by Chavan, because the divaricate lucinids are not common in North America. Chavan restricted the name *Divaricella* to species with lateral teeth obsolescent or absent, having well-developed, coarse divarications on the shell, a normally long anterior adductor, and a smooth inner ventral margin. He recognized two subgenera of *Divaricella: Divaricella s. s.,* which lacks laterals, is confined to the Indo-Pacific; but *Egracina,* with rudimentary laterals, has a Caribbean representative, *D. (E.) dentata* (Wood) which was included in the phenetic study. *Divalinga,* whose distinguishing characteristics were noted above, was divided by Chavan into three subgenera; two species, one Atlantic and one Pacific, of the typical subgenus were included in the phenetic study.

My observations and Chavan's data give the range of *Divalinga* as Oligocene to Recent; *Egracina,* however, has apparently not been noted from strata older than Pleistocene. It is possible that *Egracina* (and *Divaricella s. s.,* whose earliest record is Pliocene) evolved from species of *Divalinga* by increase in size and reduction of the loss of the denticulations on the ventral margin. The latter change may have been possible because the strong divarications of *Egracina* terminate in points which serrate the outer ventral margin; interlocking of these serrations may have served, as did the denticulation of the inner margin, to stabilize the articulation of the valves.

At present it seems most reasonable to treat *Divalinga* and *Egracina* as different subgenera of a single genus, *Divaricella,* in view of the probable close relationship postulated above. It is possible, however, that the subfamily Divaricellinae, which Glibert and van de Poel (1967) proposed for the divaricate lucinids and which Chavan (1969) accepted, is not a monophyletic taxon. The "Divaricellinae" are known from Late Cretaceous (Campanian) time on, with possible



Text-figure 7. Probable phylogeny of the *Myrtea* and *Anodontia* lineages. The musculature of *Myrtucina* is unknown. Approximate actual lengths of figured specimens are as follows: *Eulopia,* 5 mm; *Gardnerella* and *Eophysema,* 10 mm; *Jagonoma* and *Myrtea,* 20 mm; *Epilucina,* 25 mm; *Myrtucina* and *Nymphalucina,* 35 mm; *Anodontia,* 45 mm.

FIGURE 7.

major radiations occurring in the Eocene and the Miocene (Chavan, 1951a, 1969).

### PATTERNS IN THE EVOLUTION OF THE LUCINIDAE

The evolutionary history of the lucinids records four periods of major adaptive radiation, the "more or less simultaneous divergence of numerous lines all from much the same ancestral adaptive type into different, also diverging adaptive zones" (Simpson, 1961, p. 223). In many large-scale evolutionary studies, such as those of a phylum or a class, all the major subdivisions prove to be of about equal antiquity, and no major group can be asserted with certainty to have given rise to any other. Radiation may take place near the time of origin of a taxon, or at any subsequent time when new niches become available. The Lucinidae may exemplify a similar pattern of evolution at the family level.

Assuming that the Middle Ordovician *Babinka* gave rise to the Silurian *Ilionia,* the first major radiation of the Lucinidae appears to have occurred in Devonian time. The principal contributor to the radiation was *Paracyclas* (first known from the Middle Silurian, and and represented by a number of Devonian species). The genera *Phenacocyclas* and *Crassatellopsis* (if the latter is indeed a lucinid) are also Devonian. These taxa may all have descended from *Ilionia;* some or all may eventually be traced directly to *Babinka.* The taxonomic difficulties resulting from the poor preservation of most representatives of the Paleozoic genera preclude a more detailed assessment of the mid-Paleozoic radiation. I have noted that the *Lucina* lineage may be represented in Paleozoic time by *Phenacocyclas* and *Crassatellopsis,* and the *Miltha* lineage by *Ilionia* and *Paracyclas.*

Chavan (1952b) recognized five Jurassic lucinid genera. Of these, four *(Jagonoma, Mesomiltha, Discomiltha, Mesolinga)* are first known, in Europe, from the early or middle part of Late Jurassic time; one *(Luciniola)* is of Early Jurassic origin. The species of these taxa range in size from very small to medium (less than 10 mm to not more than 40 mm in maximum dimension), and most are concentrically sculptured (*Jagonoma* sometimes has faint radials). They show the same combinations of dentition and musculature noted in later lucinids. Species with concentric sculpture, of very small to small size, with well-developed cardinals and laterals, and with short or normally long anterior adductors *(Luciniola, Mesolinga)* may be ancestral to the *Lucina* lineage. Concentrically sculptured ones of small to medium size, with cardinals well developed but laterals obsolescent or absent, and with anterior adductor scars of normal or greater than normal length *(Mesomiltha, Discomiltha)* may belong to *Miltha. Jagonoma,* of small size, with a round or anteroposteriorly elongated shape, with cardinals and anterior laterals well developed and posterior laterals weak, and with faint radials superimposed on two orders of concentric ribs, may be ancestral to both the *Codakia* and the *Myrtea* lineages.

The Upper Jurassic radiation within the Lucinidae occurs soon after the appearance of the Thyasiridae and precedes that of the Ungulinidae (Chavan, 1969). The Mesozoic lucinoid radiation also coincides with the rise of the infaunal siphon-feeding bivalves, as documented by Stanley (1968). Stanley believed that the radiation of the siphonate bivalves was facilitated by their possession of the heterodont hinge, which is mechanically well suited for rapid burrowing in soft strata, and the eulamellibranch gill, a more efficient pumping device than the filibranch gill. I have here suggested that the Paleozoic Lucinacea may have been the ancestral heterodont-eulamellibranch stock. Paleozoic lucinoids whose dentition is known usually have cardinal teeth, but their laterals are weak or absent. Of the major groups of the Lucinacea, only the Lucinidae (and not all of them) have a fully heterodont hinge line with both cardinals and laterals; the Thyasiridae are usually edentulous and the Ungulinidae have only cardinals. Traditional schemes of bivalve evolution, such as that of Bernard (1895-1897), based on dentition characters have considered the "lucinoid type" of dentition to be the primitive heterodont type, and, as Cox (1969) pointed out, this evaluation now seems to be geologically as well as morphologically tenable. As for the eulamellibranch gill, there is of course no direct evidence as to what kind of gill the Paleozoic Lucinacea had. Conceivably, however, it was more like that of the Recent Astartidae, which have two thin demibranchs, eulamellibranch but simple in structure, being homorhabdic, nonplicate, and having little connective tissue (Saleuddin, 1965) than like the single fleshy demibranch of Recent Lucinidae. It is possible that the form of the lucinid gill is related to respiratory efficiency in poorly oxygenated environments (cf. Allen, 1958; Jackson, 1970) and thus is not so important a taxonomic character as previously believed. Boss (1970) stated that in the genus *Astarte* some species have one demibranch and others two. Some Recent species of the Leptonacea, which may be descended from the Lucinacea, have only one demibranch, whereas others have two (Leyborne Popham, 1940).

A third radiation of the Lucinidae began late in the Cretaceous and reached its fullest extent in mid-Eocene time. (The paucity of the Paleocene marine record may somewhat exaggerate the amount of differentiation which took place in the Eocene; many taxa first recorded from Eocene strata may have been of Paleocene origin.) About half the lucinid subgenera date back to this latest Mesozoic-early Cenozoic radiation. The species of this study, for example, can be allocated among 28 subgenera (30 if the early Tertiary species of *Callucina* and the late Tertiary *Parvilucina? costata* group are given subgeneric status). Of these taxa, at least 13 and perhaps as many as 16 originated at some time in the Late Cretaceous to mid-Eocene radiation (the three questionable cases are ones in which I have not been able to verify reports of an early Tertiary occurrence or in which the precise definition of a subgenus is in question). Four of the 28 subgenera — *Claibornites, Eophysema, Plastomiltha,* and *Recurvella* — are unknown after late Eocene, though the second and third, and perhaps also the first, evidently gave rise to other taxa.

In Paleogene time, the *Miltha* lineage seems to have been the most highly diversified of the lucinid lineages. Most of the large lucinids of Paleogene seas were species of *Miltha s. s., Eomiltha,* and *Plastomiltha.* The *Lucina* lineage was less diverse than it now is, and species of subgenera whose modern representatives are of medium to large size were then generally small. Such species as *Lucina (Cavilinga) pomilia* and *L. (Callucina?) papyracea* are represented by numerous individuals in the Gulf Coast Eocene. The *Codakia* and *Myrtea* lineages are poorly represented in Paleogene rocks; the *Anodontia* lineage included both small *(Eophysema subvexa)* and large *(Anodontia? augustana)* members, but was not particularly abundant in either number of species or number of individuals. Five of the 11 genus-group taxa of divaricate lucinids recognized by Chavan (1951a) appeared in the Paleogene; only two, both of Oligocene origin, survive at present. *Microloripes,* the probable ancestor of *Loripes,* is of Paleocene origin.

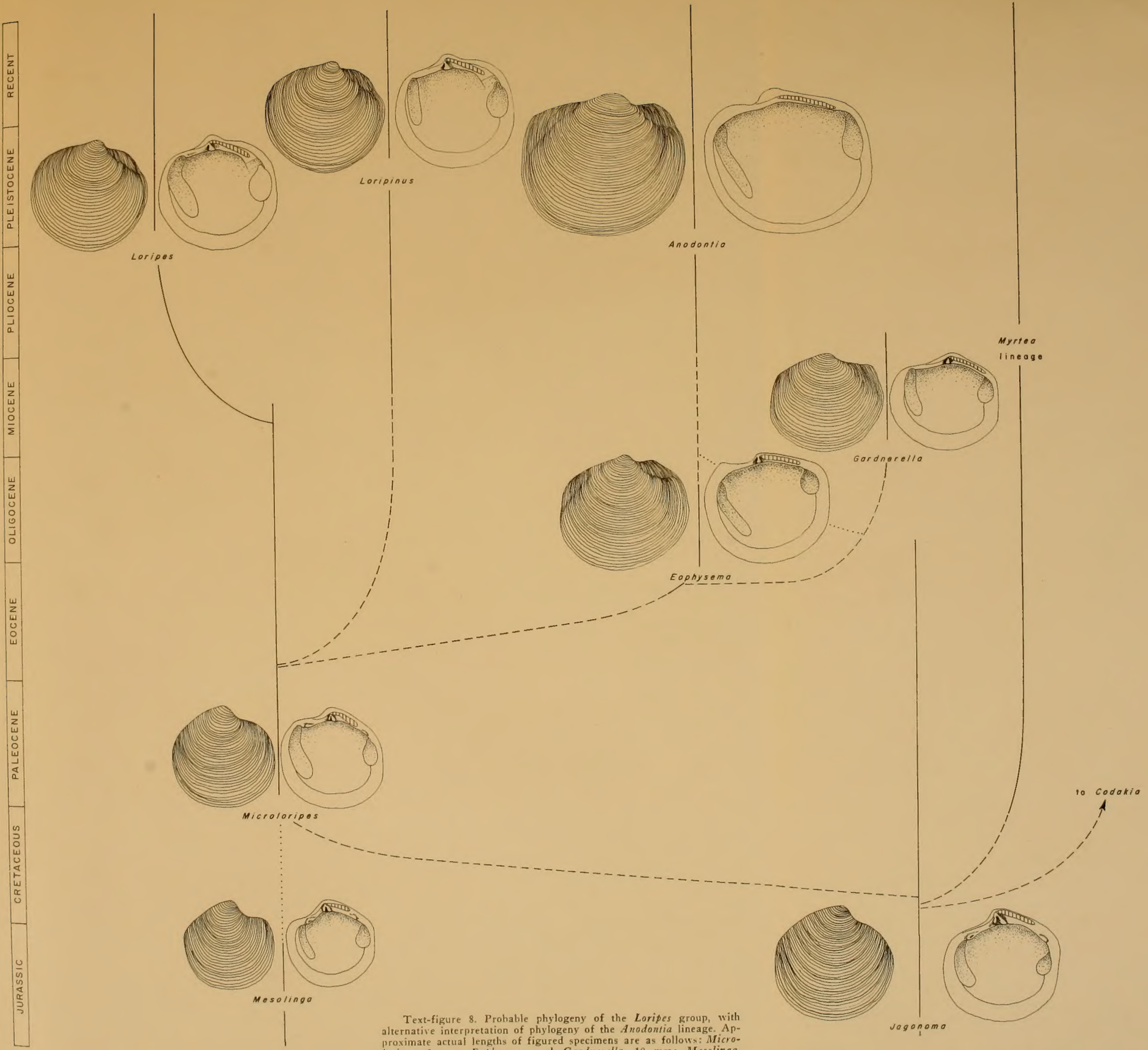
The Late Cretaceous-Paleogene generic and subgeneric radiation of the Lucinidae parallels the trend documented by Stanley (1968) for many groups of infaunal bivalves. Virtually all the superfamilies of infaunal bivalves now living are known by the end of the Cretaceous (the few exceptions are minute or deep-water forms); the rate of appearance of new genera began to increase rapidly in mid-Cretaceous time.

Near the Oligocene-Miocene boundary, a fourth lucinid radiation took place. Stewart (1930) noted that nearly all families of Tertiary bivalves and gastropods can be divided into a Paleogene and a Neogene fauna, and added that "though there is some overlapping of these two faunas it is difficult to find the ancestors of the dominant Neogene types in the [Paleogene]." Also, Stanley (1968) recognized distinct Paleogene and Neogene divisions of each of the major adaptive types of bivalves. No major lineages of the lucinids either become extinct or originate in the Neogene radiation; the differences in the faunas involve extinction of some subgenera, origin of others, and changes in the relative importance of the major lineages. As previously noted, a few subgenera disappear from the record — either by extinction or by evolutionary transformation — at the end of the Eocene. Several, such as *Miltha s. s.* and *Eomiltha,* are still extant but after the Miocene become rare. The niche of the *Miltha* lineage, in fact, may have been partly taken over by the similarly large, flattened *Codakia s. s.,* which may be of Paleocene origin but which did not become abundant until Miocene time. The great Neogene increase in diversity of *Codakia s. s.* and *Ctena* makes the *Codakia* lineage one of the dominant lucinid lineages in the Recent fauna.

The development of a number of different types of radial sculpture marks the Miocene expansion of the *Lucina* lineage. All the radially sculptured subgenera of *Lucina,* with the possible exception of *Pleurolucina,* were probably derived from the Paleogene *Callucina papyracea* group. The *Lucina* lineage is now subgenerically the most diverse of the lucinid genera.

After the Miocene, the *Myrtea* lineage apparently became confined to cold or temperate waters. The *Anodontia* lineage, which has never become diverse, continues to include a range of sizes from very small to very large species. In contrast to the situation in *Lucina,* radial sculpture is present in the Paleogene, but absent in the Neogene, members of *Anodontia.* The *Divaricella* group became more diversified in Neogene time, with a number of new subgenera coming into existence in the Miocene and later. The *Loripes* group attained its present geographic distribution — Mediterranean and Indo-Pacific — in the Neogene.

The apparent degree of difference between the Paleogene and Neogene lucinid faunas may be at least partly a function of the lack of knowledge of Oligocene lucinids. In eastern North America, the Oligocene seas were less widespread than those of either the Eocene or the Miocene (Murray, 1961). Much of the Oligocene record in this area is nonmarine, and many of the marine strata are known only from subsurface data, so that the Oligocene macrofossils are relatively inaccessible. Too, the best exposures of Oligocene marine rocks, in Alabama and Mississippi, are predominantly carbonates, in which the shells of bivalves are less well preserved than in the Eocene sands and Miocene sands which provide the classic localities for lucinids in eastern North America.



Text-figure 8. Probable phylogeny of the *Loripes* group, with alternative interpretation of phylogeny of the *Anodontia* lineage. Approximate actual lengths of figured specimens are as follows: *Microloripes*, 5 mm; *Eophysema* and *Gardnerella*, 10 mm; *Mesolinga*, *Loripes*, and *Loripinus*, 15 mm; *Jagonoma*, 20 mm; *Anodontia*, 45 mm.

FIGURE 8.

In Europe, the Tethyan geosynclinal area, which had existed since Cambrian time, began to be elevated in the Oligocene and Miocene. The destruction of the Tethyan seaway clearly accounts for many seeming anomalies in the distribution of Recent marine animals (Ekman, 1955), and, by isolating previously interbreeding populations, it may have stimulated speciation and subsequent diversification of many marine groups at the lower taxonomic levels. Increasing geographic separation of the faunas of the continental shelves of the eastern Atlantic and western Atlantic by sea-floor spreading in Cenozoic time may have had a similar effect (Valentine, 1969).

It is likely that the separation of the West Atlantic and East Pacific marine faunas by the Panamanian land bridge, and the increase in provinciality of marine faunas in Pleistocene and Recent time as a result of the unusually great latitudinal thermal gradients (Valentine, 1967) will stimulate another radiation, or at least a change in the relative dominance of various lineages, in the Lucinidae as in other marine taxa. We are, however, too close in time to see their effects at levels higher than the subspecific or specific ones.

## SYSTEMATICS

This section contains discussions of the 28 lucinid subgenera and the 42 species included in my earlier studies (Bretsky, 1970, 1971) of the relationship between numerical-taxonomic (phenetic) and evolutionary classifications. The information given for each subgenus is as follows: synonymy; authorship; type species; discussion of nomenclatural problems; diagnosis; and data on the geographic and temporal distribution of its included species and on its inferred phylogenetic relationships. The treatment of the various species discussed in detail includes a synonymy (not intended to be a complete reference to every mention of the species in the literature but covering major technical and semipopular works whose emphasis is on classification and identification rather than on stratigraphic or ecological matters); a description based on the specimens examined and measured during the compilation of character states for the phenetic study; information on the present repository of type and figured specimens; a statement on the number, age, provenance, and repository of the specimens examined for the phenetic study; and a discussion dealing with nomenclatural problems, comparisons with similar species, and ecology.

I have taken a conservative approach to the synonymization of species, because time was not available to carry out detailed investigation of either the patterns of morphological variation or the questions of nomenclatural priority which would have had to be evaluated for each of the 200-odd species casually mentioned in the sections on distribution and phylogenetic relationships of the various subgenera. Similarly, I have refrained from designating type specimens for those species discussed herein for which no unambiguous type designation has been made, in order to avoid possible conflict with a forthcoming study by Dr. Joseph C. Britton of Texas Christian University, formerly of the National Museum of Natural History, on the ecology and distribution of Recent Lucinidae.

Abbreviations for parameters measured are as follows (Text-fig. 2):

L — length
H — height
H/L — ratio of height to length
D — depth, or inflation, of one valve
D/L — ratio of depth to length
A — anterior length (length of the part of the shell in front of the beak)
A/L — anterior expansion (ratio of anterior length to total length)

Abbreviations of the names of museums are as follows:

YPM — Peabody Museum of Natural History, Yale University, New Haven, Conn.
USNM — National Museum of Natural History [United States National Museum], Washington, D.C.
ANSP — Academy of Natural Sciences of Philadelphia, Penn.
PRI — Paleontological Research Institution, Ithaca, N.Y.

### Genus **LUCINA**

### Subgenus **LUCINA**

*Egraca* Leach, 1852, p. 310.
*Linga* de Gregorio, 1885, p. 217.
? *Quasilucina* Stewart, 1930, pp. 38, 178.

*Author.* — Bruguière, 1797, pls. 284-286.

*Type species.* — *Venus pensylvanica* Linné, 1758, p. 688; designated by Schumacher, 1817, p. 165.

*Discussion.* — Chavan (1937, 1952a) and Stewart (1930) discussed the complicated problem of the choice of a type species for the genus *Lucina*. Bruguière (1797) introduced the name *Lucina* at the top of Plates 284, 285, and 286 of the *Encyclopédie Méthodique*. Though 12 species are figured on these plates, only the three figured on Plate 284 have been considered as candidates for type species of *Lucina*. Dillwyn (1817) identified these three species as follows:

Fig. 1a, b, c — *Venus pensylvanica* Linné, 1758.
Fig. 2a, b, c — *Venus jamaicensis* Chemnitz, 1784.

[Because the International Commission on Zoological Nomenclature (1944, Opinion 184) has held the work in which this name appears to be non-binomial, the objective synonym *Tellina pectinata* Gmelin (1791) is the earliest available name for this species. Because the various authors whose type designations are to be examined used the name *V. jamaicensis*, for the sake of simplicity it will also be employed in the following discussion.]

Fig. 3a, b, c — *Venus edentula* Linné, 1758.

The genus *Lucina* was never described by Bruguière, who died soon after his contribution to the *Encyclopédie Méthodique* was published (Dance, 1966). According to the International Code of Zoological Nomenclature (1964), a name published before 1931 accompanied by an illustration but not by a description, as was *Lucina*, is available. Lamarck (1799) was the first to describe *Lucina*, citing *Venus edentula* as an example of the genus. Chavan (1937, 1952a) argued that, because Lamarck had explicitly stated that his citations were only examples to clarify his generic diagnoses, the citation of *Venus edentula* should not be considered a type designation. Article 67(c)(i) of the International Code, which states: "Mention of a species as an example of a genus does not constitute a type-designation", appears to support Chavan's contention. Before the formulation of the International Code, however, the influential taxonomists Fischer (1887) and Dall (1901b) accepted Lamarck's citation of *V. edentula* as a valid type designation. The use of the name *Lucina* for the large, inflated, edentulous lucinids (here placed in *Anodontia*) thus is prevalent in much taxonomic literature.

A second description of *Lucina* by Lamarck (1801) included a citation of *Venus jamaicensis*, the only species which he listed under *Lucina*. In this work, however, Lamarck stated that he would cite "une espèce connue ou très rarement, plusieurs" to illustrate the characters of each genus. The International Commission on Zoological Nomenclature (1924, Opinion 79) has ruled, therefore, that even when only one species is cited, it cannot be construed as type of the genus. Chavan (1937) originally considered Lamarck's citation of *V. jamaicensis* as designating a type species for *Lucina*, but he later pointed out its invalidity (Chavan, 1952a).

Chavan (1937, 1952a) placed much stress on a discussion by Roissy (1805) of Bruguière's work. Roissy did not designate a type species for *Lucina*, but he named three species [*L. jamaicensis*, *L. edentula*, and *L. fimbriata* (Linné, 1758)] as typical "Lucines", removing *L. pensylvanica* to the "Tellines". Chavan claimed that the exclusion of *L. pensylvanica* indicated that this species did not accord with "the original concept of the genus" (Chavan, 1952a). Such an argument was valid when the principle of "type designation by elimination" was in force (see Blackwelder, 1967, p. 531). Under present rules of type designation Roissy's transferral of *L. pensylvanica* to another taxon does not eliminate it from consideration as the possible type species of *Lucina*. No type species having been designated for *Lucina* before 1805, all the species which Bruguière originally included in it remained available for designation as its type.

The type designation by Schumacher (1817) is the one accepted here. Schumacher frequently divided his genera into several sections, for each of which a single species was cited, though the sections were not given Latin names. Only one species was cited for each genus not divided into sections. Stewart (1930) considered that a species cited as type species for a genus which was not subdivided would qualify as type under the modern rules. *Lucina* is such a genus. Schumacher cited "*Lucina pensylvanica*. Delam. [Lamarck]" and referred to the figures of *Venus pensylvanica* Linné given by Chemnitz (1784). Chavan (1937, 1952a) did not challenge Stewart's acceptance of the general validity of Schumacher's type designations, but he did reject the designation of *L. pensylvanica* on the ground that Schumacher had considered Lamarck the author of *Lucina* and had failed to refer to Bruguière's work. Such an interpretation is inconsistent, however, with Article 67(g) of the International Code of Zoological Nomenclature, which reads as follows:

> If, in designating the type-species for a nominal genus, an author refers to an author or date other than those denoting the first establishment of the genus or the first reference of nominal species to it, he is nevertheless to be considered, if the species was eligible, to have designated the type-species correctly.

Because Schumacher chose one of the species which Bruguière included in *Lucina*, his designation of *Lucina pensylvanica* should be valid under the present Code. A possible objection may arise, however, from Schumacher's having divided some genera (though not *Lucina*) into several unnamed sections, each with its own type species. The situation does not seem, though, to be exactly analogous with Lamarck's rejected citation in which several species were given as examples of one unsubdivided genus.

Chavan (1937, 1952a) rejected two type designations subsequent to Schumacher's for analogous reasons. Schmidt (1818) designated *L. pensylvanica*, referring to Bruguière's Plate 284 but not specifying the figure number, and also referring to the figures of *L. jamaicensis* in Chemnitz (1784). Children (1823) designated *L. jamaicensis* as type; in 1937

Chavan regarded this designation as valid, but in 1952 he rejected it because Children had credited the genus to Lamarck, not Bruguière.

Stewart (1930) accepted as first valid type designation the citation by Anton (1839) of *L. pensylvanica.* In his introduction, Anton stated that the type species of each genus or subgenus would be the species whose name was printed in small capital letters. *L. pensylvanica,* cited as of Bruguière, pl. 284, fig. 1, is printed thus. Chavan's (1952a) objection to accepting Anton's type designation is based on the fact that Anton divided *Lucina* into four groups (not given subgeneric names). Each group is headed by a species whose name is printed in italics; this species is described in some detail. Other species of each group, whose names are printed in lower-case letters, are listed with only brief descriptions or references to other works. Anton's Group *c* of *Lucina* is headed by *pensylvanica* (in italics), which is also listed in small capitals as the second of four species of Group *c.* Chavan thus reasoned that *L. pensylvanica* could be interpreted only as type of the group of species which it heads, not as type of the entire genus — though it is the only species of *Lucina* whose name is printed in small capitals. Other genera, such as *Venus,* are divided into named subgenera, each with its (capitalized) type species. These subgenera are further divided into smaller groups, unnamed and headed by italicized species names. I infer that Anton intended to divide *Lucina* into informal groups but to consider it as a single genus with *L. pensylvanica* designated as type species.

Chavan (1952a) rejected the designation by Herrmannsen (1846) of *L. pensylvanica* as type species for *Lucina* Bruguière and *Lucina* Schumacher. The first designation which he considered unquestionable was that by Gray (1847). Gray designated *Venus jamaicensis* as type of *Lucina* Bruguière, also listing *Lucina* Schumacher with *V. pensylvanica* as its type species. Under Chavan's interpretation that only a citation which referred explicitly and exclusively to Bruguière's work could be considered as designating a type species for *Lucina, L. jamaicensis* was accepted as type species. The results of this interpretation had the merit of according with his earlier acceptance (Chavan, 1937) of Children's (1823) designation of *L. jamaicensis.*

I consider the type designation *Venus pensylvanica* Linné by Schumacher (1817) valid under the present code unless the citation of type species for each of several unnamed sections of some genera, not including *Lucina,* invalidates all Schumacher's type designations. Schmidt's (1818) designation may be ineligible because he may have included two different species in *L. pensylvanica;* but it would not be invalidated by his having referred to *Lucina* Lamarck rather than *Lucina* Bruguière. Similarly, there seems to be no valid objection to Children's (1823) designation of *L. jamaicensis,* which would have priority were both Schumacher's and Schmidt's designations rejected. Anton's (1839) designation of *L. pensylvanica,* which is completely in accord with his expressly outlined method of designating types, is the first to refer explicitly to Bruguière as author of the name *Lucina.*

As noted above, Dall (1901b, 1903) used the name *Lucina* for species now placed in *Anodontia;* he used the name *Phacoides* Gray [1847; a Latinization of a vernacular name proposed by Blainville (1824, 1825)] to cover a large number of lucinid species, including *L. pensylvanica* as well as its type species, *L. jamaicensis.* Chavan (1937) considered the name *Phacoides* invalid; as has been shown, he regarded *L. jamaicensis* as the type species of *Lucina.* He placed *L. pensylvanica* in *Linga* de Gregorio (1885); the type species of this genus is *Lucina columbella* Lamarck (1818) from the Miocene of France. Chavan considered *Linga* and *Lucina* (*Phacoides* of this paper) to be closely related, but he ascribed generic status to both and divided each into several subgenera. I consider, however, that the subgenera which Chavan assigned to *Linga* and *Lucina* belong to a single lineage. Because the name *Lucina* has priority, it can be used in a broad sense to cover all species of these and related subgenera. In this case, the *pensylvanica-jamaicensis* question would, if settled differently by a ruling of the International Commission on Zoological Nomenclature, change only the names to be applied to the subgenera *Lucina (Lucina)* and *Lucina (Phacoides);* it would still permit the use of the name *Lucina* as a general term for all the subgenera herein assigned to the *Lucina* lineage.

*Diagnosis.* — Shell of small to medium size, rounded, strongly inflated, anterior expansion moderate. Surface sculpture concentric, distinct to coarse, with irregularly spaced growth rings. Dorsal areas conspicuous; anterior one depressed and forming pseudo-lunule; posterior one set off by groove, whose junction with the ventral margin forms a notch in the shell outline. Lunule inconspicuous except on small individuals, produced by a shallow, "figure-8"-shaped identation under the prosogyrous beaks. Ligament long, straight, external but slightly inset. Anterior adductor scar straight, of normal length and width, closely parallel to pallial line; posterior adductor scar elliptical. Anterior pedal retractor scar separate from anterior adductor; posterior pedal retractor scar above and partly separate from posterior adductor. Hinge plate wide, with one anterior and one posterior lateral in right valve, double anterior and posterior laterals in left valve; two cardinals, of about equal size, in each value. Pallial blood vessel scar present; inner ventral margin denticulate.

*Distribution and phylogenetic relationships.* — The subgenus *Lucina* is represented in the Recent fauna by *L. (L.) pensylvanica* (Linné, 1758), found in the Caribbean Sea and along the eastern coast of the United States as far north as North Carolina; *L. (L.) adansoni* d'Orbigny, 1839b, from West Africa; and *L. (L.) despecta* E. A. Smith, 1904, from South Africa (Abbott, 1954; Lamy, 1920). *Lucina sombrerensis* Dall, 1901b, may also belong to this subgenus; but its small size, the presence of a plication which sets off the anterior third of the shell, and the curved anterior adductor scar suggest affinity with *Pleurolucina.*

*L. (L.) pensylvanica* is found in the Pleistocene of Florida (Yale Peabody Museum collections) and in the Pliocene Caloosahatchee Formation of southwestern Florida (DuBar, 1958) and beds of equivalent age at St. Petersburg, Florida (Olsson and Harbison, 1953). The subgenus *Lucina* may have reached its peak of diversity in Miocene time. The Miocene (Helvetian) species *Lucina columbella* Lamarck, 1818 [which was designated as type species of *Linga* de Gregorio, 1885, by Sacco (1901)] is widely distributed in Europe (Chavan, 1937). Both Stewart (1930) and Chavan (1937) considered *L. columbella* and *L. pensylvanica* congeneric, the principal difference between them being the smaller size of *L. columbella.* Chavan (1937) regarded the European species *L. basteroti* Agassiz, 1845 (early Miocene), and *L. strictula* Sacco, 1901 (late Miocene), as "varieties" of *L. columbella.*

Woodring (1925) listed three species of *Lucina s. s.* from the Bowden Formation of Jamaica. He assigned a middle Miocene (Helvetian) age to this abundantly fossiliferous marl. One of the species, *L. (L.) podagrina* (Dall, 1903), was divided by Woodring into two subspecies. The subspecies *podagrina s. s.* is characterized by an extreme degree of inflation (D/L of the holotype = 0.57), while *podagrina alaranta* is more moderately inflated (D/L of the holotype = 0.32). A second Bowden species, *L. (L.) browni* (Woodring) closely resembles *L. (L.) pensylvanica.* The third Bowden species, *L. (L.?) tithonis* (Dall, 1903), is similar to the Recent species *L. (L.?) sombrerensis* Dall (see above).

Other Miocene species which probably belong to *Lucina s. s.* are the following:

*Lucina densata* Conrad, 1867, from the Duplin Marl (late Miocene) of North Carolina.

*Lucina glenni* (Dall, 1903) from the Chipola Formation of Florida; Puri (1953), on the basis of foraminiferal evidence, considers this formation to be of middle Miocene age.

*Lucina wacissana* (Dall, 1903) from the late Oligocene Flint River Formation of Georgia and Suwanee Limestone of Florida, and the early Miocene Tampa Limestone of Florida.

Representatives of *Lucina s. s.* have apparently not been identified from the early and middle Oligocene of North America. In the late Eocene Ocala Limestone of Florida, however, Harris (1951) and Richards (1953) identified specimens closely resembling, perhaps conspecific with, *L. (L.) wacissana* (Dall). Chavan (1937) considered a French Oligocene species, *L. (L.) oligocaenica* (Cossmann, 1921), to be transitional between *L. (L.) carinifera* Conrad, 1833c (see below), and *L. (L.) columbella* Lamarck. A late Eocene species of *Lucina s. s.* from Colombia is *L. (L.) woodringi* B. L. Clark, 1946.

The oldest species of *Lucina s. s.* known to me are from the upper middle Eocene of Alabama. One of these, *Lucina carinifera* Conrad, 1833c, from the Gosport Sand, is the type species of *Quasilucina,* which Stewart (1930) proposed as a subgenus of *Lucina.* Though one of the criteria by which Stewart differentiated *Quasilucina* from *Lucina* was the lack of an anterior lateral in the right valve of the former, the only definitely identified specimens of *L. carinifera* which I have seen are two left valves in the Conrad type collection at the Academy of Natural Sciences of Philadelphia. Because of this ambiguity in the definition of *Quasilucina,* the subgenus was not included in the phenetic study. Except for its smaller size (length and height about 12 mm), *L. carinifera* closely resembles other species of *Lucina s. s.;* it is essentially identical with *L. (L.) pensylvanica* in sculpture, dorsal areas, lunule, musculature, and left-valve dentition. *L. (L.) hamata* (Dall, 1903), from the Lisbon Formation (middle Eocene), which underlies the Gosport Sand, may be conspecific with *L. (L.) carinifera.*

### **Lucina (Lucina) pensylvanica** (Linné)

Plate 25, figures 1-4

*Venus pensylvanica* Linné, 1758, p. 688.
*Lucina* [unnamed species], Bruguière, 1797, pl. 284, figs. 1a-c.
*Lucina pensylvanica* (Linné), Schumacher, 1817, p. 165; Schmidt, 1818, p. 56; Anton, 1839, p. 6; Herrmannsen, 1846, p. 630; Gray, 1847, p. 195; Reeve, 1850, pl. 6, fig. 29.
*Phacoides (Here) pensylvanicus* (Linné), Dall, 1901b, p. 807; Dall, 1903, p. 1367.
*Phacoides (Linga) pensylvanicus* (Linné), Lamy, 1920, p. 199.

*Lucina (Lucina) pensylvanica* (Linné), Stewart, 1930, pp. 175-178; Olsson and Harbison, 1953, p. 80; DuBar, 1958, p. 167, pl. 7, fig. 2; Abbott, 1954, p. 385, pl. 38h; Warmke and Abbott, 1961, p. 176, pl. 36a.
*Lucina aurantia* Deshayes, 1830, p. 384; Reeve, 1850, pl. 6, fig. 31.
*Lucina grandinata* Reeve, 1850, pl. 6, fig. 29.
*Lucina virgo* Reeve, 1850, pl. 6, fig. 28.

*Description.* — Shell of medium size (median length of 37 specimens 32 mm, range 8-42 mm), usually nearly round (median H/L 0.98, range 0.89-1.03), strongly inflated (median D/L 0.32, range 0.27-0.38), anterior expansion generally moderate (median A/L 0.46, range 0.35-0.54). Surface sculpture as in generic diagnosis. Periostracum yellow-brown, thin, covering entire surface of valves; elevated ridges of periostracum, which are superimposed on concentric ribs and sometimes broken up to form dorsally reflected spines, give impression of coarse surface sculpture (Plate 25, figure 1). Shell usually white; some individuals have ventral third of shell, both internally and externally, pinkish-orange. Dorsal areas, lunule, ligament, musculature, and dentition as in generic diagnosis; cardinals sometimes reduced, though not obsolescent, in larger individuals. Pallial blood vessel scar present; inner ventral margin denticulate.

*Types.* — The type specimen of *Venus pensylvanica* Linné is in the collection of the Linnean Society of London (Dodge, 1952).

*Material.* — The phenetic study was based on about 50 Recent and Pleistocene specimens from Florida and the Caribbean, deposited in the collections of the Yale Peabody Museum and the U.S. National Museum.

*Discussion.* — Deshayes's *Lucina aurantia* apparently differs from *L. pensylvanica* (Linné) only in possessing internal and external coloration. Since in several other lucinid species, individuals may have or lack color on the shell, *L. aurantia* is here synonymized with *L. pensylvanica.* The name *Lucina virgo* Reeve applies to shells which have been smoothed by post-mortem abrasion (Abbott, 1954). Reeve also proposed that the name *L. grandinata* replace *L. pensylvanica* because he "doubted whether the *Lucina Pensylvanica* really inhabits the shores from whence it derives its name"; however, emendations for such reasons have no status in nomenclature.

Stanley (1970) showed that *L. pensylvanica* lives with its anterior region uppermost and with the surface of its anterior dorsal area approximately horizontal; in other words, its orientation is rotated 90° from the "typical lucinid living position" shown in Text-figure 1.

### Subgenus **HERE**

*Author.* — Gabb, 1866, p. 28.

*Type species.* — *Lucina (Here) richthofeni* Gabb, 1866 (= *L. excavata* Carpenter, 1857), by monotypy; also by subsequent designation (Stoliczka, 1871).

*Discussion.* — Gabb (1866) proposed the subgenus *Here* for a Pliocene species which he named *Lucina (Here) richthofeni,* stating that two other species might be included in the subgenus: the Recent *L. excavata* Carpenter and "a small subglobose species with five or six large, rounded, somewhat curved ribs, found in the Gulf of California." According to Dall (1901b), *L. excavata* is the juvenile of a Recent species which Dall identified with *L. richthofeni.* Dall's synonymization of Gabb's and Carpenter's species has the advantage, as Keen (1958) pointed out, of giving the type species of *Here* a more readily pronounceable name. The small species with five or six large ribs is probably *Lucina (Pleurolucina) undatoides* Hertlein and Strong, 1945. Because Gabb definitely included only one species, *L. (H.) richthofeni,* in *Here,* the type species of this subgenus was fixed by monotypy. Doubtfully included species are not considered in determining the type species of a genus-group taxon [International Code of Zoological Nomenclature, 1964, Art. 68(c)]. Stoliczka (1871) explicitly designated *L. (H.) richthofeni* as type species of *Here.*

*Diagnosis.* — Shell of small to medium size, slightly elongate to slightly higher than long, moderately to strongly inflated, anterior expansion moderate to great. Surface sculpture concentric, growth rings irregularly spaced. Dorsal areas faint to distinct, anterior one forming pseudo-lunule. Lunule large and deeply excavated, symmetrical, almost perforating the hinge plate and forming a round pit beneath the beaks, proportionately more prominent on smaller specimens. Anterior adductor scar straight, parallel to pallial line; posterior adductor scar oval. Anterior pedal retractor scar separate from anterior adductor scar, posterior one above and partly separate from posterior adductor. Hinge plate wide; anterior and posterior laterals single in left valve, double in right. Right anterior cardinal completely, and right posterior one partly, effaced by deep lunule; two cardinals in left valve, crowded together by excavation of lunule (Plate 25, fig. 6); cardinals in larger specimens may be obsolescent. Pallial blood vessel scar present; inner ventral margin denticulate.

*Distribution and phylogenetic relationships.* — Grant and Gale (1931) gave the range of *L. (H.) excavata* Carpenter as from Oligocene to Recent. The Pleistocene and Recent forms range from San Pedro, California, to Mazatlan, Sinaloa, Mexico. The Miocene and Oligocene representatives of the species were found in southern California. The Oligocene occurrence, reported in a faunal list in Wagner and

Schilling (1923), may be questionable because no figure of the species was provided; however, the lunule of *L. (H.) excavata* is so distinctive that the species is unlikely to have been misidentified.

A late Eocene species from Colombia, *Lucina (Here) colombiana* B. L. Clark, 1946, seems, from Clark's figures and descriptions, to resemble closely *L. (H.) excavata.*

The ancestors of *Here* may have resembled a middle Miocene species, *L. (Lucina) glenni* (Dall, 1903), from the Alum Bluff Group of Florida. Dall (1903, p. 1366) stated that juvenile specimens of this species have a deeply excavated lunule which becomes relatively inconspicuous, "obscured by the gyrate beaks", in the adults. Though *L. (L.) glenni* appears too late in the stratigraphic record to be directly ancestral to *Here, Here* may have descended from a similar species in which the deepening of the lunule persisted throughout ontogeny.

Chavan (1942) proposed the name *Herella,* as a subgenus of *Here,* for the French lower Eocene (Cuisian) species *Lucina levesquei* Deshayes, 1860. Species which he included in *Herella* range in age from Paleocene to Oligocene (Chavan, 1969). The specimen figured by Deshayes externally resembles *Lucina s. s.* and *Here,* except that the dorsal areas are less conspicuous; the lunule is deep, possibly excavated, and apparently effaces the cardinals of the right valve. The lateral teeth are absent or rudimentary.

Olsson (1932) proposed the name *Illesca,* as a subgenus of *Lucina,* for a late Eocene species, *Phacoides (Here) andersoni* Olsson, 1930a, from Peru. This species resembles *H. excavata* in dentition and in the deeply excavated lunule, but is smaller, and has no surface sculpture except for about six regularly spaced concentric growth rings, so deeply incised that the segments into which they divide the shell seem to imbricate. A similar, though not so strong, development of growth rings occurs also in the subgenus *Cavilinga,* which apparently also originated in Eocene time, and which has a deep but not excavated lunule. It appears reasonable at present to consider both *Herella* and *Illesca* subgenera of *Lucina,* probably most closely related to *Here.*

### **Lucina (Here) excavata** Carpenter

Plate 25, figures 5-10

*Lucina excavata* Carpenter, 1857, p. 98; Gabb, 1866, p. 29; Brann, 1966, p. 37, pl. 12, fig. 140; Keen, 1968, p. 396, pl. 56, fig. 23.
*Lucina (Here) excavata* Carpenter, Stewart, 1930, pp. 180-182, pl. 15, fig. 3, pl. 17, fig. 5; Grant and Gale, 1931, pp. 290-291, pl. 14, figs. 2, 5, 10; Palmer, 1958, p. 86; Keen, 1958, p. 94, fig. 188; Olsson, 1961, p. 208, pl. 29, figs. 7, 7a.
*Here excavata* (Carpenter), Valentine, 1961, pp. 332, 334.
*Lucina (Here) richthofeni* Gabb, 1866, p. 29; Gabb, 1869, pl. 8, figs. 49, a, b; Stoliczka, 1871, p. 251.
*Phacoides (Here) richthofeni* (Gabb), Dall, 1901b, pp. 805, 810, 827, pl. 40, figs. 7, 9; Dall, 1903, p. 1361; Lamy, 1920, pp. 171, 202.
*Phacoides richthofeni* (Gabb), Arnold, 1907, p. 543, pl. 45, fig. 4; Wagner and Schilling, 1923, pp. 243, 244.
*Linga (Here) richtofeni* [*sic*] (Gabb), Chavan, 1937, pp. 202-205, fig. 3.

*Description.* — Shell of small to medium size (median length of 5 specimens 18 mm, range 9-23 mm), slightly elongate to slightly higher than long (median H/L 0.94, range 0.91-1.08), moderately to strongly inflated (median D/L 0.31, range 0.27-0.48), anterior expansion moderate to great (median A/L 0.49, range 0.46-0.53); shape changing throughout ontogeny, with smaller specimens moderately inflated and longer than high, larger ones strongly inflated and higher than long (cf. figures 5 and 9, Plate 25). Periostracum thin, brown. All other characters as in generic diagnosis.

*Types.* — The original specimens of *Here excavata* are included in the collection made by Frederick Reigen at Mazatlán; the shells of the Reigen collection are in the British Museum (Natural History), 1 type (Keen, 1968, p. 396, pl. 56, fig. 23) Carpenter (1857) described them in his "Catalogue of the Mazatlan Shells in the British Museum". His illustrations, which were never published during his lifetime, were deposited in the U.S. National Museum. Doris C. Brann recently wrote an introduction to these illustrations; this is the work referred to as Brann (1966) in the synonymy above. The lectotype of *Here richthofeni,* designated by Stewart (1930), is ANSP 4492 in the Academy of Natural Sciences of Philadelphia. This articulated specimen is the original of Gabb's (1869) figure 49 and of plate 15, figure 3 of Stewart (1930). The specimen figured by Dall (1901b, pl. 40, figs. 7, 9) is USNM 108828 (it is Pl. 25, figs. 9, 10 of this paper).

*Material.* — The phenetic study was based on about 10 Recent specimens, from Southern California and Baja California, in the collections of the National Museum of Natural History. The lectotype in the Academy of Natural Sciences of Philadelphia, from the Pliocene Pico Formation, San Fernando, California, was subsequently examined.

*Discussion.* — On the basis of data from Recent occurrences and Pleistocene paleoecology, Valentine (1961) listed *L. (Here) excavata* as a member of his protected sandy shore (intertidal) and shallow inner sublittoral associations. The latter association is also a sandy-bottom assemblage.

## Subgenus **PHACOIDES**

*Dentilucina* Fischer, 1887, p. 1143.

*Author.* — Gray, 1847, p. 195 (after Blainville, 1824, p. 334; Blainville, 1825, p. 550 — vernacular name).

*Type species.* — *Tellina pectinata* Gmelin, 1791, p. 3236 (= *Venus jamaicensis* Chemnitz, 1784, p. 24 — proposed in nonbinomial work); by monotypy (in synonymy).

*Discussion.* — Although Blainville (1828, 1825) coined the name "Phacoides", Gray (1847) was the first to use it in a way which complies with modern rules for introducing a generic name. Blainville (1825) divided the genus *Lucina* into five groups, for each of which he gave a brief description. His first group was characterized by its lenticular shape, concentric ribbing, strongly indicated dorsal areas, and variable and sometimes absent hinge teeth. After the description the words "Les L. Phacoides" appear in parentheses. *Lucina jamaicensis* is cited as an example, with a reference to plate 284, figures 2a, b, c, of Bruguière. The name "Phacoides" is apparently used in a vernacular sense. Of the remaining four subdivisions of *Lucina,* Blainville identified three with previously named genera and gave no name to the fourth; evidently, then, "Phacoides" was not intended as a new generic name.

The name "Phacoides" apparently was not used again until the 1840's. In 1846, Agassiz cited it in a bibliographic reference to Blainville, 1825, in the *Nomenclator Zoologicus.* Agassiz evidently considered "Phacoides" a valid generic name, but he did not designate a type species nor list any included species. Gray (1847), in his "List of the Genera of Recent Mollusca, their synonyma and types", regarded *Venus jamaicensis* as type species of *Lucina* Bruguière [on the basis of Lamarck's (1801) description of *Lucina* which cited this species (see above)]. He placed "Phacoides, Blainv. 1825" in synonymy with it. Many authors have interpreted this citation by Gray as an implicit Latinization of and type designation for "Phacoides". Chavan (1937, 1952a), however, believed that Gray's synonymic usage of "Phacoides", and a similar citation by Adams and Adams (1858), should be treated only as quotations from Blainville. He also argued that the plural number of Blainville's term "Les L. Phacoides" implied that more than one species belonged to the group, and thus *L. jamaicensis* could not be considered the type by monotypy. The current Code, however, states [Art. 69(a)(i)] that "originally included species" available for designation as type comprise only those actually cited by name. Chavan believed that the name "Phacoides" had not been validly introduced into taxonomic nomenclature prior to Fischer's (1887) proposal of *Dentilucina* as a subgenus of *Lucina* with *L. jamaicensis* as type species. Because Chavan considered *L. jamaicensis* the type species of *Lucina,* in any event he regarded both *Phacoides* and *Dentilucina* as junior objective synonyms of *Lucina.* Under the interpretation here accepted that *Lucina pensylvanica* is the type species of the genus *Lucina* and its nominate subgenus, a name is still required for the *L. jamaicensis* group.

The section of the Code dealing with the publication of names in synonymy [Art. 11(d)] states that:

> A name first published as a synonym is not thereby made available unless prior to 1961 it has been treated as an available name with its original date and authorship, and either adopted as the name of a taxon or used as a senior homonym.

Dall (1901b) was apparently the first worker to use the name *Phacoides* extensively. As previously stated, he considered *Venus edentula* Linné the type of *Lucina.* He placed about three-fourths of the lucinid species which he discussed in his "Synopsis of the Lucinacea" in *Phacoides,* dividing this genus into many subgenera and sections. Particularly when early twentieth-century literature is taken into account, *Phacoides* is probably the name most widely used for lucinid bivalves, both among biologists and among paleontologists. *Dentilucina,* conversely, has been little used, and then only as a subgeneric name. Stewart (1930) accepted Gray's listing of *Phacoides* in the synonymy of *Lucina* as the first use of it as a generic name, and stated that *L. jamaicensis* could be considered its type species; certainly Stewart's discussion fulfills the nomenclatural requirement that a name first published as a synonym must be "treated as an available name with its original date and authorship" to be made available.

*Diagnosis.* — Shell of medium to large size, generally longer than high, moderately inflated, with a moderate anterior expanion. Surface sculpture consisting of two types of concentric ribs: first-order concentrics distinct, coarse or rugose, elevated, spaced several millimeters apart; second-order concentrics consisting of several fine lamellae between each two first-order concentrics (Plate 26, figure 1). Growth rings, when present, irregularly spaced. Lunule triangular, slightly or distinctly asymmetrical. Anterior adductor scar long, narrow, straight, close to pallial line. Posterior adductor scar round. Anterior pedal retractor scar separate from adductor, posterior one above and partly separate from adductor. Hinge of right valve with one or two cardinals and one anterior and one posterior lateral; left valve with two cardinals and double anterior and posterior laterals. Cardinals obsolescent in larger specimens; conversely, laterals (especially anterior ones) well developed in large specimens. Pallial blood vessel scar present; inner ventral margin finely denticulate or smooth.

*Distribution and phylogenetic relationships.* — The subgenus *Phacoides* seems to have been primarily European and

Indo-Pacific throughout its history. Only about three species of the subgenus *Phacoides* as here delimited have been identified from North America, although the name *Phacoides* has frequently been used in a broad sense, following Dall (1901b, 1903). Lamy (1920) and Chavan (1937) listed five Recent species which I would include in the subgenus *Phacoides*. Of the four whose habitats are given, three are Indo-Pacific; the type species, *Lucina (Phacoides) pectinata* Gmelin, 1791, is from the western Atlantic.

Chavan (1937) traced the European record of *Phacoides* continuously from early Eocene (Cuisian) through Pliocene time. He stated that the European species generally were smaller and had better developed cardinals than *L. (P.) pectinata*. Later Chavan (1947) described a species (*Lucina blanckenhorni* Chavan) of the subgenus from Cretaceous (Campanian) rocks of Jerusalem. From his figures and descriptions, this species seems to differ from other species of *Phacoides* only in having less conspicuous dorsal areas.

The Recent North American species *L. (Phacoides) pectinata* was reported from the Pliocene and early Miocene of Florida (Olsson and Harbison, 1953; Mansfield, 1937). Dall (1903) described specimens from several Miocene localities as *Phacoides (Phacoides) domingensis*. The type specimen of this species is from a horizon of unknown age — the National Museum of Natural History label bears the words "Bowden horizon" — in the Dominican Republic. A fragmentary valve from the middle Miocene Bowden Formation of Jamaica was believed by Woodring (1925) to represent a distinct species, unnamed because of its poor preservation. Of the specimens from the early Miocene Tampa Limestone of Florida which Dall had assigned to *P. domingensis*, Mansfield (1937) provisionally placed one in *P. pectinatus* and proposed a new species of *Lucinisca* to include the rest.

Olsson (1964) described *Lucina (Phacoides) pacifica* from beds of probable early Miocene age in Ecuador. This species, which is similar to *L. (P.) pectinata*, is the only *Phacoides* known from the eastern Pacific area; the subgenus is not represented in the Recent West Coast fauna. The earliest Western Hemisphere species which probably belongs to *Phacoides* is *Lucina fortidentalis* Harris, 1896, from the early Paleocene Clayton Formation of Georgia and Alabama. Like the Cretaceous *L. (P.) blanckenhorni* Chavan, 1947, it is smaller and has fainter dorsal areas than do younger species of *Phacoides;* the dentition, surface sculpture, and musculature are consistent with assignment to *Phacoides*. *Lucina mattiformis* Stephenson, 1941, from the Late Cretaceous Navarro Group of Texas, may belong to *Phacoides;* but the interior of the shell of this species is unknown.

Some subgenera here placed under *Miltha* have certain similarities to *Phacoides*. Both *Lucinoma* (Miocene-Recent) and *Plastomiltha* (Eocene) have surface sculpture consisting of two orders of concentric ribs, and have a long, narrow anterior adductor. *Plastomiltha,* unlike *Lucinoma,* also has distinct to conspicuous dorsal areas. One of the distinguishing features of the *Miltha* lineage as defined here is the presence of strong cardinals, with the lateral teeth obsolescent or completely lacking. Lucinids such as *Lucina s. s., Here,* and *Phacoides* which have laterals and whose cardinals are partially reduced are probably derived from Mesozoic taxa whose cardinals and laterals were about equally prominent. Such a group could, of course, also have given rise to the *Miltha* lineage. Stratigraphic evidence, however, indicates that the *Lucina* and *Miltha* lineages both go back to at least early Mesozoic time.

### **Lucina (Phacoides) pectinata** (Gmelin)

Plate 26, figures 1-5

*Venus jamaicensis* Chemnitz, 1784, pp. 24-25, pl. 39, figs. 408-409 (non-binomial work); Dillwyn, 1817, p. 193.
*Lucina* [unnamed species], Bruguière, 1797, pl. 284, figs. 2a, b, c.
*Lucina jamaicensis* [Chemnitz], Lamarck, 1801, p. 124. Children, 1823, p. 34, pl. 5, fig. 48; Blainville, 1825, p. 550; Anton, 1839, p. 6; Gray, 1847, p. 195; Reeve, 1850, pl. 2, figs. 7a, b; Adams and Adams, 1858, p. 467, pl. 113, figs. 4-4a.
*Lucina (Dentilucina) jamaicensis* (Lamarck), Fischer, 1887, p. 1143.
*Phacoides (Phacoides) jamaicensis* (Lamarck), Lamy, 1920, pp. 173-175; Woodring, 1925, p. 117.
*Lucina (Anodontia) jamaicensis* (Lamarck), Stewart, 1930, pp. 179-180.
*Lucina (Lucina) jamaicensis* (Lamarck), Chavan, 1937, p. 241; Chavan, 1952a, p. 119.
*Tellina pectinata* Gmelin, 1791, p. 3236; Wood, 1815, p. 169.
*Phacoides (Phacoides) pectinatus* (Gmelin), Dall, 1901b, pp. 805, 807; Dall, 1903, p. 1363; Thiele, 1935, p. 866; Abbott, 1954, p. 388, pl. 38g; Warmke and Abbott, 1961, p. 177, pl. 36b.
*Phacoides (Phacoides)* cf. *pectinatus* (Gmelin), Olsson and Harbison, 1953, p. 82, pl. 12, figs. 3, 3a, 4, 4a.
? *Phacoides (Phacoides)* cf. *pectinatus* (Gmelin), Mansfield, 1937, pp. 240-241.
*Lucina funiculata* Reeve, 1850, pl. 7, fig. 40.

*Description.* — Shell thick, large (medium length of 23 specimens 43 mm, range 15-61 mm), longer than high (median H/L 0.92, range 0.84-1.00), moderately inflated (median D/L 0.25, range 0.20-0.30), anterior expansion moderate (median A/L 0.43, range 0.35-0.48). Surface sculpture distinct, concentric, consisting of first-order raised lamellae with five or six closely spaced, fine second-order lamellae between each two first-order concentrics (Plate 26, fig. 1); growth rings usually absent, irregularly spaced when present. Dorsal areas conspicuous, set off by grooves; anterior one also marked by change in sculpture (concentric lamellae crowded together). External shell color brown or orange. Lunule long, wide, triangular, shallow, slightly asymmetrical. Ligament external. Anterior adductor scar very long, narrow, straight, parallel to pallial line. Posterior adductor scar round. Anterior pedal retractor scar separate from adductor, posterior one above and partly separate from adductor. Hinge plate wide; laterals present, anterior one sometimes very large; laterals single in right valve, double in left. Cardinals obsolescent, sometimes almost completely absent in larger individuals. One slightly bifid cardinal in right valve, two cardinals in left. Shell interior orange in color, with deeper color on hinge plate, rim of shell outside pallial line, and posterior adductor scar; interior often thickened and pustulose. Pallial blood vessel scar present; inner ventral margin usually smooth, sometimes finely denticulate.

Some specimens (Plate 26, figures 4 and 5) diverge from the above description by having a chalky, smooth exterior without clearly defined coarser and finer concentrics; a distorted appearance resulting from the beak's being placed far forward (A/L less than 0.40); dorsal areas less clearly delimited; a wider anterior and a more elongate posterior adductor scar, both chalky-white in color; an exaggerated "*Phacoides*-type" hinge line with almost no trace of cardinals and with a much more rounded and prominent anterior lateral in the right valve; and a very thick, internally pustulose shell. Some specimens are like normal *pectinata* in all respects except for the aberrant hinge line. As yet I have no indication of what ecological features may account for these variations in shape, dentition, and musculature.

*Types.* — Unknown.

*Material.* — The description is based on about 30 Recent specimens from Florida, Texas, and the West Indies, all in the Yale Peabody Museum collections.

*Discussion.* — The specific names used by Chemnitz, in the *Conchylien-Cabinet* of Martini and Chemnitz, have been ruled invalid by the International Commission on Zoological Nomenclature (Opinion 184, 1944) because the principles of binomial nomenclature were not consistently applied throughout this work. Chemnitz's name *Venus jamaicensis* was apparently first used in a proper binomial fashion by Lamarck (1801). Because Chemnitz took the name from a manuscript label in Spengler's collection, some authors have credited *V. jamaicensis* to Spengler.

Dall (1901b, 1903), recognizing Chemnitz's names to be non-binomial, employed the first valid substitute name, *Tellina pectinata* Gmelin, 1791. *Venus jamaicensis* and *Tellina pectinata* are objective synonyms because both Chemnitz and Gmelin cited plate 300, fig. 137 in Lister's (1685-1692) *Historia Conchyliorum* as illustrating their respective species.

Dall (1901b) stated that *L. (P.) pectinata* ranges from Florida to Montevideo, Uruguay; Abbott (1954) gave its northernmost extent as North Carolina. According to Stanley (1970), it inhabits intertidal and shallow subtidal, often grassy, environments. Its tolerance to stressful nearshore conditions may be related to the presence of hemoglobin in its gills, facilitating respiration in environments subject to stagnation (Read, 1962; Jackson, 1973).

### Subgenus **STEWARTIA**

*Author.* — Olsson and Harbison, 1953, p. 82.

*Type species.* — *Lucina anodonta* Say, 1824, pp. 146-147, pl. 10, fig. 9; by original designation.

*Discussion.* — Olsson and Harbison (1953) proposed *Stewartia* (as a subgenus of *Phacoides*) for "the Neogene and Recent species such as *Phacoides anodonta* and *floridana*" which had formerly been referred to the European Eocene and Oligocene genus *Pseudomiltha* Fischer, 1887; *Pseudomiltha* evidently is an edentulous member of the *Miltha* lineage. Stewart (1930) stated that the North American species placed in *Pseudomiltha* belonged to "an edentulous group of *Lucina*", but he did not propose a generic name for this group.

*Diagnosis.* — Shell of medium to large size, rounded, flat to moderately inflated, anterior expansion moderate. Surface sculpture fine, concentric, with irregularly spaced growth rings. Dorsal areas faint or distinct, never as conspicuous as those of *Lucina s. s.* Lunule deep, triangular; size of lunule variable. Ligament external. Musculature like that of *Lucina s. s.*: anterior adductor scar of normal lucinid length and width, straight, closely paralleling pallial line; posterior adductor scar elongate; anterior pedal retractor scar separate from adductor, posterior one above and partly separate from adductor. Hinge plate wide; hinge edentulous. Pallial blood vessel scar present. Inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — Several Tertiary and Recent species from eastern North America belong to *Stewartia*. Apparently the only Recent species is *L. (S.) floridana,* found living from western Florida to Texas (Abbott, 1954). Representatives of this species from the Pleistocene of Florida are also present in the Yale Peabody Museum collections. Olsson and Harbison (1953) introduced the name *Phacoides (Stewartia) anodonta intermixta* for Pliocene specimens from western Florida which are intermediate between the Recent *L. floridana* and the

Miocene type species, *L. (S.) anodonta* Say. The latter species is abundant in the middle Miocene Choptank and Calvert Formations of Maryland and Virginia; Mansfield (1932) also reported it from the late Miocene Choctawhatchee Formation of Florida. Less common in the Choptank and Calvert Formations is a smaller, more inflated species, *L. (S.) foremani* Conrad, 1842. *L. (S.) paranodonta* (Gardner, 1926), from the middle Miocene Oak Grove Sand and Shoal River Formation of Florida, is probably conspecific with *L. (S.) anodonta*. *Phacoides (Pseudomiltha) wongi* Olsson, 1914, from the upper Miocene Choctawhatchee Formation of Florida, closely resembles *L. (S.) foremani.*

*Miltha (Megaxinus) gluminda* Woodring, 1925, from the middle Miocene Bowden Formation of Jamaica, resembles *L. (S.) anodonta* in size, shape, and sculpture; its internal characters are not known. The earliest American species which seems to belong to *Stewartia* is *Phacoides (Pseudomiltha) nocariensis* Kellum, 1926, from the early Miocene Trent Marl of North Carolina. Except for its smaller size and narrower anterior adductor scar, it closely resembles *L. (S.) anodonta.*

Undoubted species of *Stewartia* apparently are not known from deposits older than Miocene. Chavan (1938, 1969) considered *Stewartia* synonymous with *Megaxinus* Brugnone, 1880, which Chavan (1938) formerly made a subgenus of *Saxolucina* Stewart, 1930 (which he regarded as related to *Miltha*). The identity of *Megaxinus,* however, is uncertain. Brugnone included two species in *Megaxinus: Lucina rostrata* Pecchioli (the type) and *L. transversa* Bronn, 1832. Lamy (1920) incorrectly considered *L. transversa* the type species of *Megaxinus;* Chavan (1938) placed this species in *Gibbolucina* Cossmann, 1904. Unfortunately, neither Brugnone, Lamy, nor Chavan (1938) gave any bibliographic reference to Pecchioli's work. Chavan (1969) cited "*L. rostrata* Pecchioli, 1864" but did not give a fuller reference; his drawing of *L. rostrata* (Chavan, 1969, Fig. E3, 5a, 5b), presumably after Pecchioli, shows only internal features; there are traces of anterior laterals and of cardinals, and the shell appears to be more elongate dorsoventrally and to have a more elevated beak than does *L. (S.) anodonta.* Dall (1903), after examining specimens from Brugnone's collection, concluded that *Megaxinus* is a thyasirid. Chavan (1969) gave the range of *Megaxinus* as from Oligocene to Recent and placed it in the subfamily Lucininae. The Recent *Miltha (Megaxinus) tellinoides* (Reeve, 1850), from tropical West America, as figured by Keen (1958), externally resembles *Stewartia.*

The similarity between the shell interiors of *L. (L.) pensylvanica, L. (S.) anodonta,* and *L. (S.) floridana* is striking (cf. Pl. 25, fig. 2; Pl. 26, fig. 7; Pl. 26, fig. 11). Externally there is less resemblance, because the dorsal areas of *Stewartia* are not conspicuous; *pensylvanica* and *floridana,* however, both have a thin yellow periostracum.

A possible close relative of *Lucina s. s.* and *Stewartia* is *Lucina (Lepilucina) gratis* Olsson (1964, p. 47, pl. 7, figs. 1-1c) from the middle Miocene Angostura Formation of Ecuador. *Lepilucina* has dentition like than of *Lucina s. s.,* and musculature like that of *Lucina s. s.* and *Stewartia.* It is similar in size, shape, and inflation to *Lucina s. s.* The anterior dorsal area is conspicuous, but the posterior one is less well defined; the lunule resembles that of *Stewartia.* The surface sculpture consists of rugose concentric ribs.

### **Lucina (Stewartia) anodonta** Say

Plate 26, figures 6-8

*Lucina anodonta* Say, 1824, pp. 146-147, pl. 10, fig. 9; Conrad, 1840, pp. 39-40, pl. 20, fig. 4; Tuomey and Holmes, 1857, p. 55, pl. 18, fig. 2.
*Phacoides (Pseudomiltha) anodonta* (Say), Dall, 1903, p. 1378; Glenn, 1904, p. 90, figs. 3, 4; Gardner, 1926, p. 113.
*Saxolucina (Megaxinus) anodonta* (Say), Chavan, 1938, p. 79.
*Phacoides (Stewartia) anodonta* (Say), Olsson and Harbison, 1953, p. 82.
*Phacoides (Pseudomiltha) paranodonta* Gardner, 1926, p. 113, pl. 20, figs. 3-5.
*Phacoides (Stewartia) anodonta intermixta* Olsson and Harbison, 1953, pp. 82-83, pl. 12, fig. 2.

*Description.* — Shell large (median length of 31 specimens 46 mm, range 35-56 mm), usually round (median H/L 0.98, range 0.91-1.05), flat (median D/L 0.18, range 0.14-0.22), anterior expansion moderate (median A/L 0.46, range 0.38-0.54). Sculpture concentric, all ribs equally prominent with growth rings irregularly spaced (the apparent regular spacing of growth rings or coarse concentric lamellae in Say's figure is an exaggeration). Anterior and posterior dorsal areas faint. Lunule poorly defined, short, narrow, deep, slightly asymmetrical. Ligament external. Anterior adductor scar of normal length and width, straight, closely paralleling pallial line; posterior adductor scar elliptical. Anterior pedal retractor scar separate from adductor; posterior one above and partly separate from adductor. Hinge plate wide; no cardinal or lateral teeth. Pallial blood vessel scar present, emphasized in many individuals by thickening of rest of shell interior (Plate 26, figs. 7, 8); inner ventral margin smooth.

*Types.* — Say's type specimen of *Lucina anodonta* consists of both valves in the John Finch Collection in the British Museum (Natural History), No. L. 13198.

*Material.* — The phenetic study was based on about 60 specimens from the middle Miocene Calvert Formation and Choptank Formation of Maryland and Virginia, in the collections of the Yale Peabody Museum. Specimens subsequently examined at the National Museum of Natural History and Paleontological Research Institution were also from the Calvert Formation and Choptank Formation, except for a few from the late Miocene Choctawhatchee Formation of Florida (USNM 361629) and Yorktown Formation of Virginia (PRI 3081).

*Discussion.* — *Lucina (Stewartia) anodonta* occurs in all five of the members in which Gernant (1970) subdivided the Choptank Formation, but it is most common in the three middle members, which Gernant considered to represent inner shelf and marginal marine regimes. *L. (S.) anodonta* is rare in the lowermost and uppermost, presumably deeper-water members.

### **Lucina (Stewartia) floridana** Conrad
Plate 26, figures 9-11

*Lucina floridana* Conrad, 1833a, p. 344.
*Phacoides (Pseudomiltha) floridana* (Conrad), Dall, 1901b, p. 808; Dall, 1903, pp. 1378-1379.
*Pseudomiltha floridana* (Conrad), Lamy, 1920, pp. 92-94, text-fig.
*Saxolucina (Megaxinus) floridana* (Conrad), Chavan, 1938, p. 79.
*Phacoides (Stewartia) floridana* (Conrad), Olsson and Harbison, 1953, pp. 82-83.
*Lucina (Pseudomiltha) floridana* (Conrad), Abbott, 1954, pp. 387-388, pls. 30aa, 38i.
? *Lucina barbata* Reeve, 1850, pl. 4, fig. 16a, b.

*Description.* — Shell of medium size (median length of 30 specimens 32 mm, range 22-42 mm), slightly elongate to round (median H/L 0.97, range 0.90-1.02), flat to moderately inflated (median D/L 0.20, range 0.17-0.22), anterior expansion moderate (median A/L 0.45, range 0.39- 0.51). Has more distinct dorsal areas and a better-defined, wider, and deeper lunule than *L. (S.) anodonta,* and lacks the secondary thickening of the shell interior. Periostracum similar in color and texture to that of *L. (L.) pensylvanica* but thinner and more patchy than in that species, and not concentrically ribbed or spinose.

*Types.* — Conrad's original specimens, if still extant, are probably in the Recent mollusk collections of the Academy of Natural Sciences of Philadelphia; in a brief visit to that institution I was unable to locate them.

*Material.* — The phenetic study was based on about 40 Recent and Pleistocene specimens from Florida, in the collections of the Yale Peabody Museum.

*Discussion.* — Abbott (1954) gave the range of this species as "west coast of Florida to Texas". Lamy (1920) synonymized *Lucina barbata* Reeve, 1850, with it; Reeve's descriptions and figures are consistent with an assignment to *L. (S.) floridana*, but Reeve gave no habitat data.

### Subgenus **CALLUCINA**

*Author.* — Dall, 1901b, p. 806.

*Type species.* — *Lucina radians* Conrad, 1841, p. 347, by original designation.

*Discussion.* — Dall (1901b) proposed *Callucina* as a subgenus of *Phacoides* and divided it into two sections, *Callucina s. s.* and *Epilucina.* Chavan (1937) removed *Epilucina* from *Callucina,* revised the definition of *Callucina* to comprise only species similar to *L. radians,* and considered it a subgenus of *Lucina* (= *Phacoides*). He originally included about 30 species, ranging in age from Lower Jurassic to Recent, in *Callucina;* in an appendix to his study of the lucinids (Chavan, 1938), Chavan removed the Mesozoic species to *Mesomiltha,* which he proposed as a new subgenus of *Cavilucina* Fischer, 1887. Later he raised *Callucina* to generic rank and proposed two new subgenera of it, *Callucinopsis* and *Pseudolucinisca* (Chavan, 1959b). He also placed some of the species previously assigned to *Callucina* in *Callucinella,* which he proposed as a new subgenus of *Parvilucina* (Chavan, 1961). The types of *Callucinopsis* and *Callucinella* are European Eocene species; that of *Pseudolucinisca* is Australian and Recent. Chavan's (1969) figured in the *Treatise on Invertebrate Paleontology* representing these three taxa are drawings showing only the hinge lines and musculature; not having seen either original specimens of the types of these subgenera nor any good illustrations of them, I have not attempted to apply these names to any of the North American material treated in this study.

*Diagnosis.* — Shell of very small or small size, shell length rarely exceeding 20 mm, usually between 5 and 15 mm; rounded, moderately to strongly inflated, anterior expansion moderate. Surface sculpture variable; usually both concentric and radial, with radials prominent over entire shell surface, or sculpture may be concentric only. Dorsal areas generally faint. Lunule long, wide, shallow, triangular, slightly to strongly asymmetrical. Ligament external. Size and shape of anterior adductor scar variable: either of normal length and straight, or short and curved. Posterior adductor scar elliptical. Anterior pedal retractor separate from adductor, posterior one above and partly separate from adductor. Hinge plate narrow; lateral teeth sometimes present, but usually obsolescent or completely absent; right valve with reduced anterior and normal posterior cardinal, or with only one cardinal; two cardinals in left valve. Pallial blood vessel scar present. Inner ventral margin denticulate.

*Distribution and phylogenetic relationships.* — The only living North American species of *Callucina* appears to be the type species. *Lucina (Callucina) radians* was reported from the Pliocene of South Carolina (Tuomey and Holmes, 1857) and the Pliocene of Florida (Dall, 1903). Conrad's type specimen was collected in North Carolina, presumably from strata of late Miocene age (Dall, 1903).

A Pliocene species which probably belongs to *Callucina* is *Codakia (Jagonia) umbonicosta* Weisbord, 1964, from the Mare Formation of probable early Pliocene age in Venezuela. *Lucina (Callucina) camaronensis* Olsson, 1964, from the Esmeraldas Formation (late Miocene or early Pliocene) of Ecuador, closely resembles *L. (C.) radians* except that it has radials which are prominent over the entire shell surface, not just dorsally and anteriorly.

The subgenus *Callucina* seems to have reached its maximum diversity in middle Miocene time. From the middle Miocene Bowden Formation of Jamaica, Woodring (1925) identified *L. (C.) pauperata pauperata* Guppy, 1896; *L. (C.) p. oligocostata* (Woodring), and *L. (C.) eurycostata* (Woodring). These three taxa are probably conspecific. Differences in the inflation and in the strength of radials, thought to distinguish the two subspecies of *pauperata,* are within the range of variation shown by different individuals of *L. (C.) radians* from a single locality. *L. (C.) eurycostata* may be a juvenile of *pauperata.* It is about half the size of the latter and has stronger radials; but it simply may not have reached the size at which the radial ribs become indistinct.

*L. (C.) cala* (Gardner, 1936), from the middle Miocene Shoal River Formation of Florida; *L. (C.) radians* var. *medioamericana* (Olsson, 1922), from the middle or late Miocene Gatun Formation of Costa Rica; and *L. (C.) quincula* Olsson, 1964, from the Angostura Formation of probable middle Miocene age in Ecuador, definitely belong to *Callucina.*

*"Phacoides" actinoides* Maury, 1910, from the Oak Grove Sand (middle Miocene) of Florida, resembles *L. (C.) radians* in shape, musculature, and surface sculpture. Another middle Miocene species, *"Phacoides" prunoides* Maury, 1910, from the Chipola Formation of Florida, is similar in size, shape, musculature, and sculpture to *L. (Callucina) papyracea* Lea (see Text-figure 9). The presence of lateral teeth in *actinoides* and *prunoides* may indicate affinity with *Parvilucina.*

The only Oligocene species known to me which possibly belongs to *Callucina* is *Lucina choctavensis* Meyer, 1886, from the middle Oligocene Vicksburg Group of Mississippi. The holotype, a left valve (USNM 644600), closely resembles *"Phacoides" prunoides* Maury.

Chavan (1937) placed the middle Eocene species *Lucina papyracea* Lea in *Callucina;* that assignment is continued here. Possible late Eocene descendants of this species are *Lucina curta* Conrad, 1865a, and *L. subcurta* Harris, 1946, both from Mississippi; a possible ancestor of it is *Lucina ulrichi* Harris, 1897 (early Eocene, Alabama). Placement of these species in *Callucina* is based mostly on their dentition, particularly on the virtual or complete absence of lateral teeth. Their short, curved anterior adductor scar is like that of Recent species of *Parvilucina;* they differ from Recent species of both *Parvilucina* and *Callucina* in having only concentric sculpture. *Lucina uhleri* W. B. Clark, 1895, from the Paleocene Aquia Formation and lower Eocene Nanjemoy Formation of Maryland, probably does not belong to this group of species, although Clark and Martin (1901) considered *L. ulrichi* and *L. uhleri* synonymous.

Some small, concentrically sculptured species, such as *Lucina chatfieldiana, L. seminalis,* and *L. oleodorsum* Stephenson, 1941, from the Upper Cretaceous (Maestrichtian) Navarro Group of Texas, may belong to *Callucina.* These species, however, are represented only by articulated specimens; because no internal features are known, even their placement in the Lucinidae may be questioned.

The subgenera *Parvilucina* and *Callucina* appear to be closely related, perhaps originating from a common ancestor in Late Cretaceous or early Tertiary time. Further evidence of this relationship will be considered in the discussion of *Parvilucina.*

### **Lucina (Callucina) radians** Conrad

Plate 27, figures 1-4

*Lucina radians* Conrad, 1841, p. 347; Tuomey and Holmes, 1857, p. 57, pl. 18, figs. 4, 5; Holmes, 1860, p. 28, pl. 6, fig. 3.
*Phacoides (Callucina) radians* (Conrad), Dall, 1901b, pp. 809, 824-825, pl. 42, fig. 8; Dall, 1903, pp. 1380-1381; Lamy, 1920, p. 170; Thiele, 1935, p. 866; Olsson and Harbison, 1953, p. 85, pl. 7, fig. 3; DuBar, 1958, p. 167, pl. 7, fig. 7; Warmke and Abbott, 1961, p. 177, pl. 36j.
*Phacoides (Lucinoma) radians* (Conrad), Dall and Simpson, 1901, p. 494.
*Lucina (Callucina) radians* (Conrad), Chavan, 1937, p. 249.
*Lucina radiata* Conrad, 1845, p. 70, pl. 40, fig. 3.
? *Phacoides radians* var. *medioamericanus* Olsson, 1922, pp. 221-222, pl. 32, fig. 16.

*Description.* — Shell small (median length of 24 specimens 15 mm, range 10-22 mm), slightly longer than high (median H/L 0.97, range 0.87-1.05), moderately inflated (median D/L 0.28, range 0.25-0.33), anterior expansion moderate (median A/L 0.47, range 0.42-0.54). Sculpture dominantly concentric; radial ribs usually prominent only in umbonal region, bifurcating. Growth rings irregularly spaced. Periostracum of Recent specimens thin, grayish.

Dorsal areas faint. Lunule long, wide, triangular; lunule asymmetrical, with widest part in right valve and longest part in left. Anterior adductor of normal length and width, straight, parallel to pallial line; posterior adductor elongate. Anterior pedal retractor separate from adductor, posterior one partly separate. Hinge plate narrow, with no laterals; one cardinal, or occasionally two with the anterior one being small, in right valve; two cardinals in left valve. Pallial blood vessel scar present. Inner ventral margin denticulate.

*Types.* — E. J. Moore (1962) listed one right valve (ANSP 30603) in the Cenozoic mollusk collections of the Academy of Natural Sciences of Philadelphia as the "possible holotype" of *Lucina radians* Conrad.

*Material.* — The phenetic study was based on about 30 Recent and Pleistocene specimens, from North Carolina, Florida, and Haiti, in the collections of the Yale Peabody Museum and the National Museum of Natural History. The possible type specimen at the Academy of Natural Sciences of Philadelphia, and some Miocene specimens from North Carolina and South Carolina at the Paleontological Research Institution, were subsequently examined.

*Discussion.* — The strength of the radial ribs is variable in this species; in some individuals they are scarcely visible, and in others they are prominent on the dorsal half of the shell, especially anteriorly. The figure given by Dall (1901b) exaggerates their prominence somewhat. Warmke and Abbott (1961) gave the geographic distribution of living representatives of this species as the southeastern United States and Puerto Rico, stating that the species is moderately common just offshore. The late Miocene representatives of *Lucina (Callucina) radians,* on which the species name is based, are essentially indistinguishable from the Recent ones.

### **Lucina (Callucina) papyracea** Lea

Plate 27, figures 5-7

*Lucina papyracea* Lea, 1833, p. 58, pl. 1, fig. 31; Conrad, 1834, p. 7; Harris, 1919, pp. 116-117, pl. 38, figs. 17-21.
*Phacoides papyraceus* (Lea), Dall, 1903, p. 1362.
*Lucina (Callucina) papyracea* Lea, Chavan, 1937, p. 253.
*Lucina modesta* Conrad, 1846b, p. 403, pl. 4, fig. 13.

*Description.* — Shell very small (median length of 15 specimens 4.8 mm, range 3.9-8.3 mm), thin, shape variable but generally rounded (median H/L of 21 specimens 0.98, range 0.90-1.08), strongly inflated (median D/L of 15 specimens 0.31, range 0.28-0.38), anterior expansion moderate (median A/L of 21 specimens 0.47, range 0.36-0.54). Surface sculpture concentric, fine; growth rings irregularly spaced. Dorsal areas faint. Lunule long, triangular, wide, slightly asymmetrical, shallow. Ligament external. Anterior adductor scar unusually short, curved. Posterior adductor scar elliptical. Anterior pedal retractor scar separate and posterior one partly separate from adductor. Hinge plate narrow, with laterals completely absent or, occasionally, poorly defined. One cardinal tooth in right valve, two in left. Pallial blood vessel scar present; inner ventral margin denticulate.

*Types.* — Lea's holotype (ANSP 5164) and 14 of his paratypes (ANSP 5165-5178) are in the Academy of Natural Sciences of Philadelphia. The type of *L. modesta* Conrad, which Harris (1919) synonymized with *L. papyracea,* is missing from the Philadelphia Academy collection (E. J. Moore, 1962).

*Material.* — The phenetic study was based on about 25 specimens, from the middle Eocene Gosport Sand of Alabama, in the collections of the Yale Peabody Museum. Lea's types at the Philadelphia Academy, and the specimens figured by Harris, which are at the Paleontological Research Institution, were subsequently examined.

*Discussion.* — Chavan's assignment of this species to *Callucina* seems to have been based on the similarity of its dentition — the virtual or complete absence of lateral teeth and the presence of only one cardinal tooth in the right valve — to that of *L. (Callucina) radians.* The short, curved anterior adductor is like that of *L. (Parvilucina) tenuisculpta,* the type species of *Parvilucina;* but the latter species has two cardinals in the right valve (though the anterior one is small) and has lateral teeth. *L. (C.) papyracea* differs from both *L. (C.) radians* and *L. (P.) tenuisculpta* in the absence of radial sculpture.

Harris (1946) traced the evolution of *L. (C.) papyracea* through Eocene time. *Lucina ulrichi* Harris, 1897, from the lower Eocene Hachetigbee Formation of Alabama, was the earliest species which he assigned to this lineage; *L. papyracea* Lea the second; and *L. curta* Conrad, 1865, from the upper Eocene Moodys Branch Formation of Mississippi, the youngest. Dall (1903) placed *L. curta* in *Myrtea* on the basis of the spinose projections on the posterior dorsal area; but, as Harris (1946) pointed out, these spines are present only on some individuals and are less regularly arranged than are those of *Myrtea spinifera.* [Harris (1946) also proposed another specific name, *L. (Myrtea?) subcurta,* for some Moodys Branch specimens which I believe are probably conspecific with *L. curta.*] Harris's type specimen of *L. ulrichi* is missing from the Paleontological Research Institution (Brann and Kent, 1960). But examination of his figures of *L. ulrichi,* of the specimens of *L. papyracea* and *L. curta* in the Philadelphia Academy, and of specimens in the PRI identified by him as *L. curta* and *L. subcurta,* verify his establishment of a close relationship between these species. All have concentric sculpture and a short, curved muscle scar, and in all the laterals are weak or absent.

The Paleocene-lower Eocene species *Lucina uhleri* Clark, 1895, is probably not a member of the *L. (C.) papyracea* lineage, although Clark and Martin (1901) provisionally synonymized *L. uhleri* and *L. ulrichi.* Harris (1919) considered them to be specifically distinct. *L. uhleri* probably has its closest affinities with *Myrtea.*

### Subgenus **PARVILUCINA**

*Author.* — Dall, 1901b, p. 806.

*Type species.* — *Lucina tenuisculpta* Carpenter, 1864b, p. 642, by original designation.

*Discussion.* — Dall proposed *Parvilucina* as a subgenus of *Phacoides,* with two sections, *Parvilucina s. s.* and *Bellucina.* Chavan (1937) later treated both these sections as subgenera of *Linga* (= *Lucina* of this paper). More recently (Chavan, 1961), he accorded generic status to *Parvilucina* and to *Callucina* [which in 1937 he considered a subgenus of *Lucina* (= *Phacoides* of this paper)] and stated that these two genera of small lucinids are closely related. As indicated in the discussion of *Callucina,* there are several early Tertiary species which seem to have affinities with both groups. Furthermore, some of the species previously assigned to *Ctena* may actually be most closely related to species of *Parvilucina.*

*Diagnosis.* — Shell of very small size, rounded or slightly longer than high, strongly inflated, anterior expansion generally moderate. Sculpture usually consisting of concentric and radial ribs, concentrics slightly stronger than radials, and radials on all parts of shell equally prominent; some species with concentric sculpture only; growth rings irregularly spaced; dorsal areas faint to distinct. Lunule generally long, wide, and triangular. Anterior adductor scar most commonly short and curved, sometimes of normal length and straight. Posterior adductor scar elliptical. Anterior pedal retractor scar separate and posterior one partly separate from adductors. Hinge plate narrow; anterior and posterior laterals well developed, single in right valve and double in left; usually two cardinals in each valve, right anterior cardinal usually much smaller than right posterior one, sometimes absent. Pallial blood vessel scar present; inner ventral margin denticulate.

*Distribution and phylogenetic relationships.* — The type species of *Parvilucina* is a Recent species found in the eastern Pacific, particularly in cold waters. Specimens of *Lucina (Parvilucina) tenuisculpta* in the National Museum of Natural History collections range from the Bering Sea to San Diego, California. Two other Recent species, *L. (P.) approximata* (Dall, 1901b), found from Monterey, California, to Panama; and *L. (P.) mazatlanica* Carpenter, 1857, which ranges from the Gulf of California to Panama, may be conspecific with *L. (P.) tenuisculpta.*

In the western Atlantic and Caribbean, *Parvilucina* is represented by *L. (P.) multilineata* Tuomey and Holmes, 1857, originally described from the Pliocene of South Carolina. This species also occurs in the Pliocene Playa Grande Formation of Venezuela (Weisbord, 1964) and in the Pliocene Caloosahatchee Formation and late Miocene Choctawhatchee Formation of Florida (Olsson and Harbison, 1953; Mansfield, 1932).

Two Recent species generally assigned to *Ctena* are here provisionally placed in *Parvilucina;* they are *Lucina costata* d'Orbigny, 1846, and *Codakia (Jagonia) portoricana* Dall, 1901b. Dall (1901b) noted a close resemblance between the two species and remarked that the second is "about half way between a typical *Jagonia* [*Ctena*] and a *Parvilucina*". Both occur in the Caribbean, and Dall (1903) also reported *L. (Parvilucina?) portoricana* from the Pliocene Caloosahatchee Formation. Evidence for the assignment of these species of *Parvilucina* is presented in the discussion of *L. (P.?) costata.* Other Pliocene species of *Parvilucina* are *L. (P.) ephraimi* Weisbord, 1964, from Venezuela; and, probably, *L. (P.) callosana* Pilsbry and Olsson, 1941, the internal features of which are unknown.

*Parvilucina* is particularly abundant in Miocene, especially middle Miocene, strata. Two late Miocene species of *Parvilucina* are *Lucina crenulata* Conrad, 1840, which ranges from Virginia to Florida (it is also found in the middle Miocene St. Marys and Calvert Formations of Maryland and Virginia) and *Lucina multistriata* Conrad, 1843, from North Carolina. *L. multistriata* has been considered a subspecies of *L. (Cavilinga) trisulcata* Conrad, 1841 (*e. g.,* by Dall, 1903); but the lunule, dentition, musculature, and faint radial sculpture of the type specimen (ANSP 30632) indicate affinity with *Parvilucina.* Conversely, *Phacoides (Parvilucina) prunus* Dall, 1903, from the middle Miocene Chesapeake Group of Maryland, is probably a synonym or a subspecies of *L. (C.) trisulcata* (see discussion of that species).

Most of the middle Miocene species here placed in *Parvilucina* were described from the Alum Bluff Group of Florida or the Bowden Formation of Jamaica. Gardner (1926) considered the Alum Bluff Group to consist of three formations: the Chipola Formation, which she correlated with the European Burdigalian (late early Miocene) and the Oak Grove Sand and overlying Shoal River Formation, both considered of Helvetian (early middle Miocene) age. She attributed differences between the molluscan faunas of the three formations to changes in water temperature throughout time. Puri (1953), on the basis of foraminiferal evidence, concluded that these formations were actually contemporaneous facies, the Oak Grove Sand being nearest shore and the Chipola Formation farthest offshore (though all were considered inner neritic). He indicated a middle Miocene age for the Alum Bluff Group but did not suggest a more specific correlation with the European Cenozoic section.

The middle Miocene age of the Bowden Formation is that indicated by Woodring (1925) in his monograph on its molluscan fauna. Dall (1903) considered the Bowden Oligocene in age, but Woodring correlated it with the European Helvetian. The lucinids of the Alum Bluff and the Bowden are similar, and it seems reasonable to consider the two lithologic units contemporaneous.

The Alum Bluff and Bowden species which may be placed in *Parvilucina* can be placed for convenience in three morphologically distinct subgroups, as follows:

A. Species closely resembling *L. (P.) tenuisculpta*
    1. Alum Bluff species
        *L. (P.) sphaeriola* (Dall, 1903)
        *L. (P.) sphaeriola angalea* (Gardner, 1926)
        *L. (P.) piluliformis* (Dall, 1903)
        *L. (P.) vaughani* (Gardner, 1926)
        *L. (P.) flumenvadosa* (Gardner, 1926)
        *L. (P.) crenulata pemphiga* (Dall, 1903)
        *L. (P.) diktyota* (Gardner, 1936)
    2. Bowden species
        *L. (P.) limnida* (Woodring, 1925)
        *L. (P.) yaquensis moratensis* (Woodring, 1925)
        *L. (Bellucina) actina* (Dall, 1903)
        *Codakia (Ctena) guppyi* Woodring, 1925 (= *L. textilis* Guppy, 1896)
B. Species closely resembling *L. (P.?) costata*
    *Codakia (Ctena) vendryesi* Dall, 1903 — Bowden
    *C. (Ctena) chipolana* Dall, 1903 — Alum Bluff
C. Species resembling both *Callucina* and *Parvilucina*
    *L. actinoides* (Maury, 1910) — Alum Bluff
    *L. prunoides* (Maury, 1910) — Alum Bluff

The species and subspecies included in the first group were for the most part defined on the basis of small differences in size, shape (particularly inflation and A/L ratios), and prominence of the radial sculpture. Dall (1903) considered *L. (Bellucina) actina* transitional between *Parvilucina* and *Bellucina;* it will be further discussed under *Bellucina.* Grant and Gale (1931) pointed out the similarity between *Codakia (Ctena) guppyi* and *L. (P.) tenuisculpta.*

Two other species of *Parvilucina* found in strata probably equivalent in age to the Bowden Formation are *Lucina (Parvilucina) yaquensis* Gabb, 1875, from the Cercado Formation of the Dominican Republic; and *L. (P.) actina* "var." *uscarensis* (Palmer, 1923), from the Uscari Shale of Costa Rica.

A possible early representative of *Parvilucina* is the early Eocene *L. (Parvilucina) sabelli* Gardner, 1927. Chavan (1937) placed several Paleocene and Eocene species in *Parvilucina;* like *L. (P.) sabelli,* these species have musculature and dentition like those of *L. (P.) tenuisculpta* but have only concentric sculpture. Text-figure 9 shows how a species such as *L. (P.) sabelli* could have given rise to the species now included in *Callucina* and in *Parvilucina.* Paleocene and Eocene species which resemble *L. (P.) sabelli* except for their lack of laterals are represented in the figure by the middle Eocene *L. papyracea;* in this paper, following Chavan (1937), they have been assigned to *Callucina.* The Oligocene *L. choctavensis* Meyer, 1886, which resembles *L. sabelli,* may descend directly from it (temporal intermediates, however, are not known in North America), or may have been derived from the *L. papyracea* group by reacquisition of laterals. Miocene radiation gave rise to *Callucina* as defined by Dall (1901b) *(pauperata, radians, prunoides, actinoides),* to *Parvilucina (sphaeriola, tenuisculpta, multilineata),* and to the group of species here provisionally placed in *Parvilucina (vendryesi, costata).* Species resembling *L. sabelli* also survived into Miocene time. The phylogeny in Text-figure 9 suggests the following subdivision of the *Callucina-Parvilucina* lineage:

*Callucina* — radial sculpture present over entire shell but most prominent on umbo and dorsal areas, or present only dorsally; anterior adductor scar of normal length, straight; laterals present or absent. Miocene-Recent. (Type species: *L. radians*)

*Parvilucina* — radial sculpture prominent over entire shell; anterior adductor short, curved; laterals present. Miocene-Recent. (Type species: *L. tenuisculpta*)

Subgenus A — radial sculpture prominent over entire shell; anterior adductor of normal length, straight; laterals present. Miocene-Recent. (Example: *L. costata*)

Subgenus B — no radial sculpture; anterior adductor short, curved; laterals present or absent. Paleocene-Miocene. (Examples: *L. sabelli, L. papyracea*)

The smallness of the anterior adductor in the early Tertiary species of this group may relate to the minuteness of their shells; *L. sabelli* is only about 3 mm long and *L. papyracea* about 5 mm. Perhaps an elongated anterior adductor was not necessary to divert the anterior inhalant current; in a very small mantle cavity, the curvature of the anterior adductor might create a current pattern which swept food particles toward the mouth. Loss of lateral dentition in the early Tertiary species seems to be correlated with thinness of the shell; for example, in the upper middle Eocene Gosport Sand *L. papyracea* is found with *L. (Cavilinga) pomilia* Conrad, a species of similar size which has a heavier shell and has strong laterals. *L. papyracea* may have inhabited more sheltered areas than *L. pomilia,* or burrowed more deeply in the substratum, so that it did not require either such a thick shell or such a stable articulation of the shell as did *L. pomilia.* (Little is known of the paleoecology of the Gosport Sand; the two species are evidently found in close association, because they are often mixed in collections, but they are so small that they probably could have undergone a good deal of reworking.) Stanley (1970), studying a Recent tidal flat, found that the edentulous, thin-shelled *Anodontia alba* burrows to greater depths than do the thicker-shelled, dentate *Lucina (Phacoides) pectinata* and *Codakia (Codakia) orbicularis.* Perhaps an analogous niche partitioning by depth zonation existed for the smaller Eocene species.

Increase in shell size in the lineages leading to *L. (Callucina) radians* and to *L. (Parvilucina?) costata* may have been correlated with the reacquisition of an anterior adductor of normal length. In the *Callucina* lineage, the increase in area of the adductor may have kept the valves stably articulated, so that laterals were not re-evolved. *Parvilucina* has retained the short, curved anterior adductor and has remained small [its largest representative, the cold-water *L. (P.) tenuisculpta,* reaches a maximum length of about 15 mm with a median of about 10 mm].

### **Lucina (Parvilucina) tenuisculpta** Carpenter

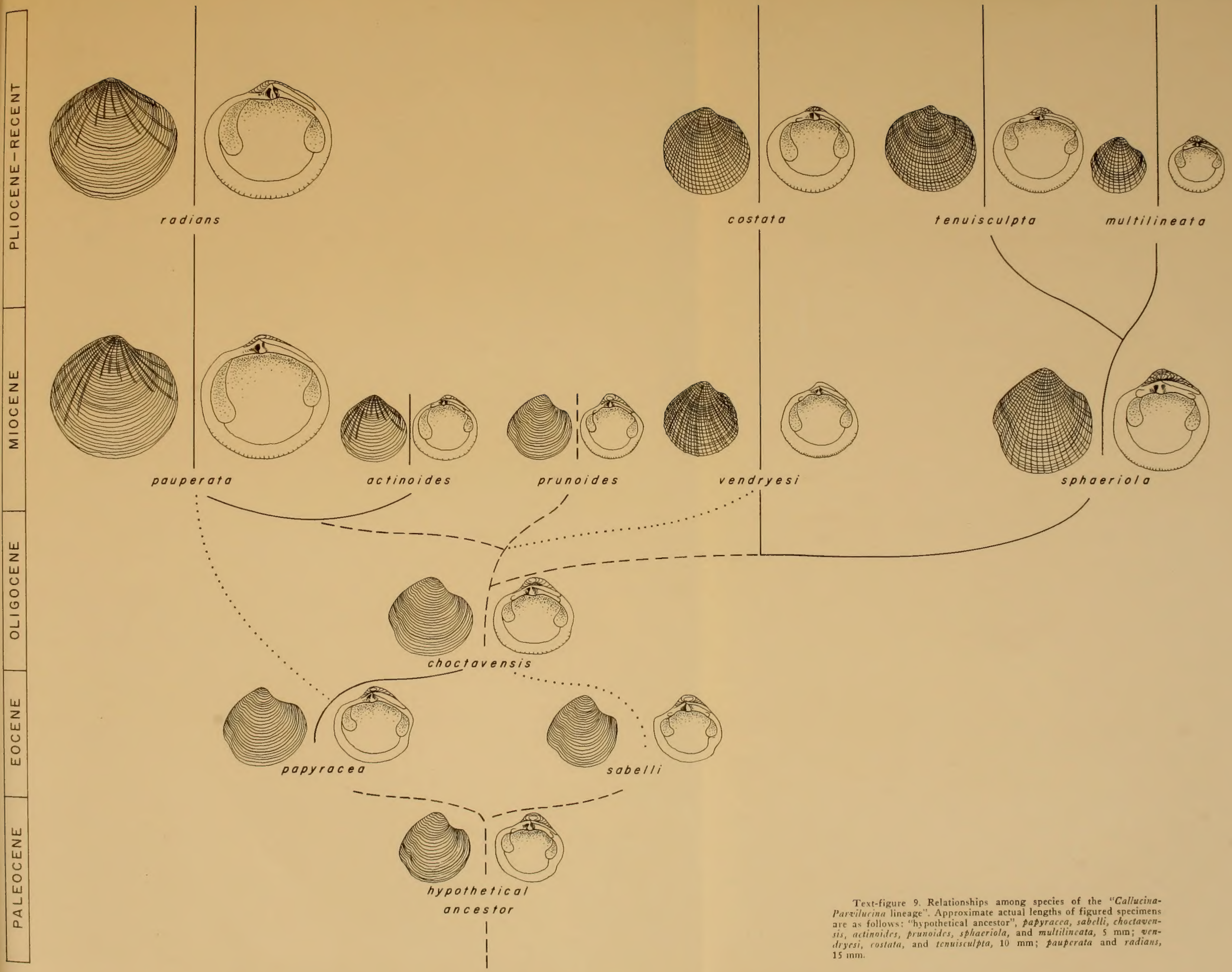
Plate 27, figures 8-13

*Lucina tenuisculpta* Carpenter, 1864b, pp. 602, 611, 642; Carpenter, 1865b, p. 57.
*Phacoides (Parvilucina) tenuisculpta* (Carpenter), Dall, 1901b, pp. 806, 828, pl. 40, fig. 5; Lamy, 1920, p. 211; Thiele, 1935, p. 865.
*Lucina (Myrtea) tenuisculpta* Carpenter, Grant and Gale, 1931, p. 288.
*Linga (Parvilucina) tenuisculpta* (Carpenter), Chavan, 1937, pp. 208-210, fig. 4.
*Lucina (Parvilucina) tenuisculpta* Carpenter, Palmer, 1958, pp. 86-87, pl. 8, figs. 8-12; Abbott, 1954, p. 387, fig. 78h.
? *Lucina mazatlanica* Carpenter, 1857, pp. 99-100; Brann, 1966, pl. 12, fig. 144.
? *Lucina (Here) mazatlanica* Carpenter, Dall, 1901b, p. 811; Lamy, 1920, pp. 202-203.
? *Lucina (Here?) mazatlanica* Carpenter, Stewart, 1930, p. 180.
? *Linga (Here?) mazatlanica* (Carpenter), Chavan, 1937, p. 204.
? *Lucina (Parvilucina) mazatlanica* Carpenter, Keen, 1958, p. 96, fig. 193; Abbott, 1954, p. 387, fig. 78g; Olsson, 1961, p. 214, pl. 31, figs. 3-3b, 9, 9a; Keen, 1968, p. 396, pl. 56, figs. 29a-b; text-figs. 5a-c.
? *Phacoides (Parvilucina) approximatus* Dall, 1901b, pp. 828-829, pl. 39, fig. 4.
? *Lucina (Myrtea) tenuisculpta* var. *approximata* (Dall), Grant and Gale, 1931, p. 289, pl. 14, figs. 8a, 8b.
? *Lucina (Parvilucina) approximata* (Dall), Olsson, 1961, p. 214, pl. 31, fig. 7.
?*Phacoides (Parvilucina) intensus* Dall, 1903, p. 1385, pl. 50, fig. 8; Grant and Gale, 1931, p. 288 [as synonym of *tenuisculpta*].

*Description.* — Shell of very small to small size (median length of 23 specimens 9.9 mm, range 6.2-14.2 mm), slightly elongate to round (median H/L 0.95, range 0.88-1.00), strongly inflated (median D/L 0.31, range 0.28-0.38), anterior expansion moderate to great (median A/L 0.49, range 0.44-0.57). Surface sculpture of concentric and radial ribs, concentric sculpture dominant; radials varying in strength from faint to distinct, but covering entire surface sculpture of shell. Growth rings irregularly spaced. Anterior dorsal area faint, defined by change in sculpture; posterior one distinct. Periostracum thin, brown, patchy; lunule long, wide, triangular, deep, asymmetrical; ligament external; anterior adductor scar short, curved, diverging from pallial line, posterior adductor scar elliptical. Anterior pedal retractor scar separate and posterior one partly separate from adductors. Hinge plate narrow, with anterior and posterior laterals single in right valve, double in left; two cardinals in each valve, right anterior cardinal usually reduced, posterior one slightly bifid. Pallial blood vessel scar present; inner ventral margin denticulate.

*Types.* — Palmer (1958, 1963) discussed the marine molluscan species described by Carpenter from the west coast of North America and Central America. The holotype of *Lucina (Parvilucina) tenuisculpta* is in the National Museum of Natural History (USNM 5244); it is figured in Plate 27, figures 11 to 13, of this paper. Of the three species tentatively synonymized above with *L. (P.) tenuisculpta,* the types of two are also in the National Museum of Natural History: *L. (P.) approximata* (Dall, 1901b) (USNM 96418); and *L. (P.) intensa* (Dall, 1903) (USNM 135041). The original specimens of *L. (P.) mazatlanica* Carpenter, 1857, are in the British Museum (Natural History) (see Brann, 1966; Keen, 1968).

*Material.* — The phenetic study was based on about 100



Text-figure 9. Relationships among species of the "*Callucina-Parvilucina* lineage". Approximate actual lengths of figured specimens are as follows: "hypothetical ancestor", ***papyracea, sabelli, choctavensis***, *actinoides, prunoides*, ***sphaeriola***, and ***multilineata***, 5 mm; ***vendryesi***, *costata*, and *tenuisculpta*, 10 mm; ***pauperata*** and *radians*, 15 mm.

FIGURE 9.

Recent specimens, including the type specimen, which was collected at Vancouver Island, British Columbia; all are housed in the National Museum of Natural History. Their distribution ranges from Nunivak Island, Alaska, to San Diego, California.

*Discussion.* — *L. (P.) approximata* and *L. (P.) mazatlanica* were distinguished from *L. (P.) tenuisculpta* largely on the basis of their smaller size and on differences in the relative strengths of the concentric and radial ribs. As indicated above, there is a good deal of variability in the prominence of the radial sculpture of specimens of *L. (P.) tenuisculpta.* If only one species is indeed involved, it has an extremely great geographic range — from Nunivak Island, Alaska, to Panama — traversing five of the six Pacific molluscan provinces recognized by Valentine (1961). Even if the southern limit of *L. (P.) tenuisculpta* is northern Baja California, as indicated by Abbott (1954), who treated *tenuisculpta* and *approximata* as different species, it remains one of the most widely ranging lucinids.

The Pliocene species *L. (P.) intensa* (Dall, 1903), based on three specimens from San Diego, California, seems to be synonymous with *L. (P.) tenuisculpta,* as indicated by Grant and Gale (1931). These authors also pointed out the similarity between *L. (P.) tenuisculpta* and *"Codakia (Jagonia)" guppyi* Woodring, 1925, from the Bowden Formation (middle Miocene, Jamaica); the latter species may be ancestral to the West Coast species of *Parvilucina.*

### **Lucina (Parvilucina) multilineata** Tuomey and Holmes

Plate 27, figures 14-16

*Lucina multilineata* Tuomey and Holmes, 1857, p. 61, pl. 18, figs. 16, 17; Holmes, 1860, p. 29, pl. 6, fig. 6; Parker, 1960, p. 334, pl. 3, figs. 21a, b.
*Phacoides (Parvilucina) multilineata* (Tuomey and Holmes), Dall, 1903, p. 1384; Mansfield, 1932, p. 101, pl. 20, figs. 6, 7; Gardner, 1944, pp. 78-79, pl. 13, figs. 34-37; Olsson and Harbison, 1953, pp. 86-87; Weisbord, 1964, pp. 221-223, pl. 29, figs. 7, 8.
*Linga (Parvilucina) multilineata* (Tuomey and Holmes), Chavan, 1937, p. 210.
*Lucina (Parvilucina) multilineata* Tuomey and Holmes, Abbott, 1954, pp. 386-387, fig. 78f.
*Lucina crenulata* Dall, 1889, p. 50 [*non* Conrad, 1840].
*Phacoides (Parvilucina) crenella* Dall, 1901b, pp. 810, 825, pl. 39, fig. 2; Lamy, 1920, p. 210.
*Lucina crenella* (Dall), Parker, 1960, p. 317.

*Description.* — Shell very small (median length of 32 specimens 4.8 mm, range 4.0-6.2 mm), slightly elongate to round (median H/L of 28 specimens 0.96, range 0.92-1.03), strongly inflated (median D/L of 32 specimens 0.38, range 0.33-0.44), anterior expansion moderate to great (median A/L of 28 specimens 0.51, range 0.44-0.69). Sculpture of concentric and radial ribs; concentrics dominant but radials also strong; radials present over entire shell surface, but on many specimens most prominent in umbonal region; growth rings frequently lacking, irregularly spaced when present. Dorsal areas distinct, anterior one forming pseudolunule. Lunule triangular, long, wide, shallow; slightly asymmetrical, greater part in right valve; ligament external. Musculature and dentition as in *L. (P.) tenuisculpta,* except anterior cardinal of right valve commonly absent. Pallial blood vessel scar present. Inner ventral margin denticulate.

*Types.* — Although some of Tuomey and Holmes' specimens are in the American Museum of Natural History, New York City, *Lucina multilineata* is not in the collection (Dr. N. D. Newell, written communication, 1971). The specimen figured by Dall (1901b) as *Phacoides crenella* is in the National Museum of Natural History (USNM 60948).

*Material.* — The phenetic study was based on about 400 Recent specimens from the Western Atlantic (North Carolina to Florida), and the Gulf of Mexico, many of which were collected by the U.S. Fish Commission's dredgings in the 1880's. These specimens, identified by A. E. Verrill, are in the Yale Peabody Museum collections. Fossil representatives of this species in the National Museum of Natural History, collected from the Pliocene Caloosahatchee Formation of Florida and the late Miocene Choctawhatchee Formation of Florida and Waccamaw Formation of North Carolina, were subsequently examined.

*Discussion.* — The synonymization of Dall's Recent and Tuomey and Holmes' Pliocene species, first suggested by Dall (1903), has been generally accepted. Weisbord (1964), who compiled data on the stratigraphic and geographic distribution of *L. (P.) multilineata,* gave its earliest appearance as late Miocene. According to him, living specimens are found "near shore to about 124 fathoms in the Gulf of Mexico from Texas to Florida and in the Western Atlantic from North Carolina to Brazil".

Gardner (1944) considered Tuomey and Holmes' name to be an error for *Lucina multistriata* Conrad, 1843. Following Dall, she treated *L. multistriata* (from the late Miocene of North Carolina) as a subspecies of *Lucina trisulcata,* the type of *Cavilinga* Chavan, 1937. Examination of the holotype of *L. multistriata* in the Philadelphia Academy collections indicates, however, that this species is a *Parvilucina.* Should *L. multilineata* Tuomey and Holmes and *L. multistriata* Conrad prove to be identical, Conrad's name would have priority.

### **Lucina (Parvilucina?) costata** d'Orbigny, 1842

Plate 28, figures 1-5

*Lucina costata* d'Orbigny, 1842, p. 296, pl. 27, figs. 40-42; d'Orbigny, 1846, p. 586.

*Codakia (Jagonia) costata* (d'Orbigny), Dall, 1901b, p. 800; Lamy, 1920, pp. 262-263.
*Jagonia (Jagonia) costata* (d'Orbigny), Chavan, 1937, p. 260.
*Codakia (Codakia) costata* (d'Orbigny), Abbott, 1954, p. 390.
*Codakia (Ctena) costata* (d'Orbigny), Warmke and Abbott, 1961, p. 178, pl. 36k.
*Lucina antillarum* Reeve, 1850, pl. 10, fig. 37.

*Description.* — Shell small (median length of 24 specimens 10.8 mm, range 7.3-13.3 mm), shape varying from somewhat elongate to slightly higher than long (median H/L 0.96, range 0.90-1.05), strongly inflated (median D/L 0.36, range 0.28-0.43), anterior expansion moderate (median A/L 0.46, range 0.38-0.53). Sculpture of radial and concentric ribs, with radial sculpture dominant; radials bifurcate near umbo, tending to occur in pairs (Plate 28, fig. 1); growth rings irregularly spaced. Anterior dorsal area faint, forming pseudo-lunule; posterior one distinct, lacking radial sculpture. Lunule short, wide, triangular, shallow, slightly asymmetrical. Ligament external. Anterior adductor scar of normal length and width, straight, parallel to pallial line; posterior adductor scar elliptical. Anterior pedal retractor separate from anterior adductor; posterior pedal retractor scar above and partly separate from posterior adductor. Hinge plate narrow; anterior and posterior laterals single in right valve, double in left. Two cardinals in each valve; right anterior cardinal considerably smaller than posterior one; right posterior cardinal slightly bifid. Pallial blood vessel scar present; inner ventral margin denticulate.

*Types.* — The original specimens of *Lucina costata* may be in the British Museum (Natural History), where D'Orbigny's Recent American collections are housed (Dance, 1966).

*Material.* — The phenetic study was based on about 30 Recent specimens, from Bermuda, Florida, and Jamaica, in the Yale Peabody Museum collection.

*Discussion.* — Dall's placement of *L. costata* in *Jagonia* (= *Ctena*) was apparently based largely on the similarity in surface sculpture. In *L. costata,* as in *Ctena mexicana* (the type species of *Ctena*), the radial ribs are bifid and the radial sculpture dominates the concentric. These species are also similar in dentition and have an external ligament. Differences in a number of other characters are shown below.

| *L. costata* | *C. mexicana* |
|---|---|
| Anterior dorsal area set off by line, forming pseudo-lunule; posterior dorsal area defined by virtual or complete absence of radials. | Dorsal areas less well defined than in *L. costata;* both set off by change in sculpture (reduction or complete loss of concentric ribs). |
| Lunule short, wide, triangular. | Lunule long, narrow, oval. |
| Anterior adductor scar of normal length and width, straight, parallel to pallial line. | Anterior adductor scar of normal length and width, but curved, diverging from pallial line. |
| Posterior pedal retractor scar partly separate from posterior adductor. | Posterior pedal retractor scar not evident. |
| Inner ventral margin denticulate. | Inner ventral margin fluted by termination of radial ribs, but not denticulate. |

In addition, species of *Ctena* are typically more compressed, more elongate, and more strongly expanded anteriorly than is *L. costata.* Comparisons of the relevant ratios (means and standard errors are given) for *L. costata* and *C. mexicana* are as follows:

*L. costata* $(N = 24)$: $H/L(\%) = 97 \pm 0.67$; $D/L(\%) = 35 \pm 0.71$; $A/L(\%) = 46 \pm 0.90$.

*C. mexicana* $(N = 10)$: $H/L(\%) = 93 \pm 1.33$; $D/L(\%) = 25 \pm 0.70$; $A/L(\%) = 52 \pm 1.74$.

The differences between the means of H/L, D/L, and A/L are all significant at a probability level of $<0.01$.

In the respects in which *L. costata* differs from *C. mexicana* — dorsal areas, musculature, lunule, shape, and denticulation of the ventral margin — it accords with many species of the *Lucina* lineage. The strong inflation, small size, and closely spaced radial sculpture suggest a relationship to *Callucina* or *Parvilucina.* The radial sculpture, which is strong over the entire shell surface, and the presence of lateral teeth are similarities with *Parvilucina;* but *L. costata* averages somewhat larger than *L. (P.) tenuisculpta,* and its long, straight anterior adductor scar is like that of *L. (Callucina) radians.* Some small individuals whose prominent radials and concentrics produce a "basket-weave" surface sculpture also resemble *Lucinisca* and *Bellucina* (cf. Plate 28, figure 5; Plate 29, figure 8; Plate 29, figure 11). The size of adults and the shape of the anterior adductor of *L. costata* are also consistent with placement in *Lucinisca;* however, *L. costata* never shows surface sculpture as coarse as that which characterizes *Lucinisca.* On the basis of similarities in dentition, sculpture, and shape (particularly its strong inflation), I have provisionally placed it in *Parvilucina.* Text-figure 9 shows the probable relationship of *L. (Parvilucina?) costata* to species of *Callucina* and *Parvilucina,* and Text-figure 5 shows the inferred relationship among *Parvilucina, Callucina, Parvilucina?, Bellucina,* and *Lucinisca.*

Species which seem to be closely related to *L. (P.?) costata,* and which are herein transferred to *Lucina (Parvilucina?),* are the following:

*Codakia (Jagonia) portoricana* Dall, 1901b. Dall (1903) stated that this species is intermediate between typical *Jagonia* (= *Ctena*) and *Parvilucina.* It ranges in age from Pliocene (Caloosahatchee Formation, Florida) to Recent. It is somewhat smaller than *L. costata* (length of the holotype, USNM 108959, about 7 mm).

*Codakia (Jagonia) vendryesi* Dall, 1903. Dall considered this species, from the Bowden Formation of Jamaica (middle Miocene), to be analogous to *L. (P.?) costata;* it is illustrated in Text-figure 9.

*Codakia (Jagonia) chipolana* Dall, 1903. This species is also middle Miocene, from the Alum Bluff Group of Florida. In his description Dall stated that in some respects, notably the well-defined dorsal areas, it resembles *Lucinisca.*

Dall (1901b) synonymized *Lucina antillarum* Reeve with *Lucina costata.*

### Subgenus **CAVILINGA**

? *Cardiolucina* Sacco, 1901, p. 89.

*Author.* — Chavan, 1937, p. 198.

*Type species.* — *Lucina trisulcata* Conrad, 1841, p. 346 (figured *in* Conrad, 1845, p. 71, pl. 40, fig. 5), by original designation.

*Discussion.* — Chavan proposed *Cavilinga* as a subgenus of *Linga* (= *Lucina* of this paper), with Conrad's Miocene species as type species. Woodring (1925) and Gardner (1926, 1944) used the name *Cardiolucina* Sacco, 1901, for *Lucina trisulcata* and related species. The type species of *Cardiolucina, Cardium agassizi* Michelotti, 1847, is a middle and upper Miocene species from Italy. From Sacco's figures it seems closely similar to *Lucina trisulcata.* Chavan (1937, p. 205), however, considered *Cardiolucina* synonymous with *Bellucina.* Because he had seen specimens of the type species of *Cardiolucina* and *Bellucina,* whereas I have not, his use of the name *Cavilinga* is followed here. What is to be included in *Bellucina* will be considered later.

According to Chavan (1937, 1938), *Cavilucina* Fischer, 1887, to which Dall referred *L. trisulcata* and related species, differs from *Cavilinga* in having an almost edentulous hinge, a short anterior adductor, and a smooth inner ventral margin. The two groups are similar in size, surface sculpture, and possession of a deep lunule. *Cavilucina* is based on a European Eocene species, *Lucina sulcata* Lamarck, 1806, of which I have not seen specimens. Although Chavan (1938) considered *Cavilucina* closest to the group which I have called the *Anodontia* lineage, it seems likely that the relationship between *Cavilinga* and *Cavilucina* is analogous to that between *Lucina* and *Stewartia.*

*Diagnosis.* — Shell of very small to small size, shape varying from longer than high to higher than long, strongly inflated, anterior expansion moderate to great. Surface sculpture fine, concentric, often with deep, regularly spaced growth rings. Dorsal areas faint to distinct. Lunule short, wide, triangular, deep, slightly asymmetrical. Anterior adductor scar of normal length and width, usually curved away from pallial line; posterior adductor scar elliptical. Anterior pedal retractor scar separate from adductor, posterior one above and partly separate from adductor. Hinge plate relatively wider in smaller species, with anterior and posterior laterals single in right valve, double in left; one or two cardinals in right valve, two in left; right posterior cardinal slightly bifid. Pallial blood vessel scar present. Inner ventral margin denticulate. Differs from *Callucina* in presence of lateral teeth; from *Parvilucina* in longer anterior adductor and generally stouter hinge plate; and from both in lack of radial sculpture and in more consistent development of growth rings.

*Distribution and phylogenetic relationships.* — *Cavilinga* is represented in the Recent fauna of the West Coast by *Lucina lingualis* Carpenter, 1864a; *Phacoides (Cavilucina) lamprus* Dall, 1901b; and *Lucina prolongata* Carpenter, 1857. The first two of these species, which Chavan (1937) and Keen (1958) placed in *Callucina,* were included in the phenetic study. Evidence that they belong to *Cavilinga* is presented later. Both are found in upper Pliocene and Pleistocene strata of Baja California (Grant and Gale, 1931; Durham, 1950).

The type species, *Lucina trisulcata* Conrad, is recorded from middle Miocene time to the Recent, though the living West Indian species are sometimes treated as a separate species or subspecies, *blanda* (Dall, 1901b). Conrad's material was probably collected from the upper Miocene Duplin Marl of North Carolina; the species has also been recorded from the middle Miocene Choptank Formation and Calvert Formation of Maryland (Glenn, 1904), and the Pliocene Waccamaw Formation of South Carolina (Tuomey and Holmes, 1857; Gardner, 1926), Caloosahatchee Formation of Florida (Olsson and Harbison, 1953), and Mare Formation of Venezuela (Weisbord, 1964). Another late Miocene species of *Cavilinga* is *Phacoides (Cardiolucina) postalveatus* Gardner, 1944, from the Yorktown Formation of Virginia.

Dall and Gardner named several middle Miocene species which seem closely related to, if not conspecific with, *Lucina (Cavilinga) trisulcata.* They are as follows:

*Phacoides (Cavilucina) trisulcatus* var. *whitfieldi* Dall, 1903 — a new name for specimens identified as *L. trisulcata* by Whitfield (1894) from well borings of Miocene age in New Jersey.

*P. (Cardiolucina) parawhitfieldi* Gardner, 1926 — Oak Grove Sand, Alum Bluff Group, Florida.

*P. (Cavilucina) recurrens* Dall, 1903 — Bowden Formation, Jamaica.

*P. (Parvilucina) prunus* Dall, 1903 — Calvert Formation and St. Marys Formation, Maryland.

Dall (1915) also recorded *P. (C.) recurrens* from the Tampa Limestone of Florida, now considered early Miocene in age. Though evidently no Oligocene or late Eocene species of *Cavilinga* have been recorded, the subgenus is abundantly represented in the upper middle Eocene Gosport Sand of Alabama. Apparently only one species — *Lucina pomilia* Conrad, 1833c — is present, but it is highly variable in shape and surface sculpture; striking variants have been named *L. alveata* Conrad, 1833c, and *L. smithi* Meyer, 1886. Harris (1919) also reported *L. pomilia* from the lower Eocene "Lignitic Stage" of Alabama; his specimens were collected from the Nanjemoy Formation and Hachetigbee Formation, upper Wilcox Group (Palmer and Brann, 1965).

*Cavilinga* was probably derived from the *Callucina-Parvilucina* line in late Paleocene or early Eocene time; it differs from the hypothetical ancestor of these two subgenera only in its more elongate anterior adductor and in the frequent occurrence of deeply impressed growth rings. The significance of the latter character is discussed under *L. (C.) trisulcata.*

### **Lucina (Cavilinga) trisulcata** Conrad

Plate 28, figures 6-15

*Lucina trisulcata* Conrad, 1841, p. 346; Conrad, 1845, p. 71, pl. 40, fig. 5; Tuomey and Holmes, 1857, p. 62, pl. 18, figs. 18, 19; Holmes, 1860, p. 28, pl. 6, fig. 4; Whitfield, 1894, p. 64, pl. 10, figs. 1-4.

*Phacoides (Cavilucina) trisulcatus* (Conrad), Dall, 1901b, p. 808; Dall, 1903, p. 1367; Lamy, 1920, p. 206.

*Phacoides (Cavilucina) trisculcatus* var. *trisulcatus* (Conrad), Dall, 1903, p. 1370.

*Phacoides (Here) trisulcatus* (Conrad), Glenn, 1904, p. 337, pl. 90, figs. 7-9.

*Phacoides (Cardiolucina) trisulcatus* (Conrad), Gardner, 1926, pp. 108-109, pl. 18, figs. 11-13.

*Linga (Cavilinga) trisulcata* (Conrad), Chavan, 1937, pp. 198-199.

*Phacoides (Cavilinga) trisulcatus* (Conrad), Olsson and Harbison, 1953, pp. 85-86, pl. 7, figs. 4, 4a, 4b.

*Lucina* [*Carilinga* (misspelled)] *trisulcata* Conrad, Warmke and Abbott, 1961, p. 176.

*Phacoides (Cavilucina) trisulcatus* var. *blandus* Dall, 1901b, p. 808; Lamy, 1920, p. 206.

*Phacoides trisulcatus* var. *blandus* Dall, Dall and Simpson, 1901, p. 493, pl. 58, fig. 13.

*Phacoides (Cavilucina) blandus* Dall, Dall, 1903, p. 1369.

*Linga (Cavilinga) trisulcata* var. *blanda* (Dall), Chavan, 1937, p. 201.

*Lucina* [*Carilinga* (misspelled)] *blanda* (Dall), Warmke and Abbott, 1961, p. 176, pl. 36d.

*Lucina (Cavilinga) trisulcata blanda* (Dall), Weisbord, 1964, pp. 214-216, pl. 28, figs. 1-4.

*Phacoides (Cavilucina) recurrens* Dall, 1903, p. 1369, pl. 52, fig. 11; Dall, 1915, p. 138, pl. 24, fig. 3.

*Phacoides (Cardiolucina) recurrens* Dall, Woodring, 1925, p. 122, pl. 16, figs. 7, 8.

*Linga (Cavilinga) recurrens* (Dall), Chavan, 1937, p. 200.

*Phacoides (Cavilucina) trisulcatus* var. *whitfieldi* Dall, 1903, p. 1370; Gardner, 1926, p. 109, 110.

*Phacoides (Cardiolucina) parawhitfieldi* Gardner, 1926, pp. 109-110, pl. 18, figs. 14, 15.

*Phacoides (Parvilucina) prunus* Dall, 1903, p. 1384, pl. 52, fig. 8; Glenn, 1904, pp. 340-341, pl. 90, fig. 3; Mansfield, 1932, p. 97.

*Linga (Cavilinga) pruna* (Dall), Chavan, 1937, pp. 201-202.

not *Lucina multistriata* Conrad, 1843, p. 307; Conrad, 1845, p. 71, pl. 40, fig. 6.

?not *Phacoides (Cavilucina) trisulcatus* var. *multistriatus* (Conrad), Dall, 1903, p. 1370.

*Phacoides (Cardiolucina) trisulcatus multistriatus* Mansfield, 1932, p. 96, pl. 20, figs. 15, 16; Gardner, 1944, p. 76, pl. 13, figs. 25-26 [not *Lucina multistriata* Conrad].

*Description.* — Shell of very small to small size (median length of 10 specimens 9.6 mm, range 6.0-11.8 mm); shape variable, ranging from longer than high to higher than long (median H/L 1.06, range 0.93-1.23); strongly inflated (median D/L 0.34, range 0.32-0.44), anterior expansion moderate to great (median A/L 0.50, range 0.45-0.59). Surface sculpture of fine to distinct concentric ribs, often also with from one to seven deeply impressed growth rings; growth rings, when present, generally regularly spaced. Dorsal areas faint to distinct. Lunule short, wide, triangular, deep, slightly asymmetrical. Ligament external. Anterior adductor scar of normal length and width, curved away from pallial line; posterior adductor scar elliptical. Anterior pedal retractor scar separate and posterior one partly separate from adductors. Hinge plate narrow, with anterior and posterior laterals single in right valve, double in left; right valve with only one cardinal, or two cardinals with anterior one very much reduced; right posterior cardinal slightly bifid; two cardinals in left valve. Recent specimens may have pink or orange interior. Pallial blood vessel scar present. Inner ventral margin denticulate.

*Types.* — The holotype of *Lucina trisulcata* Conrad may be in the Academy of Natural Sciences of Philadelphia, but neither E. J. Moore (1962) nor I was able to find it. Syntypes of *Phacoides trisulcatus* var. *blandus* Dall are in the National Museum of Natural History (USNM 17677); they include a large left valve labeled "figd. specimen", which is probably that figured as plate 58, figure 13, of Dall and Simpson, and two smaller valves. These specimens are figured in Plate 28, figures 13 to 15, of this paper. Type specimens of the other species here synonymized with *L. trisulcata* are also in the National Museum.

*Material.* — The phenetic study was based on the following specimens: two middle Miocene (Calvert Formation, Maryland) and one Recent (Florida) specimens of *L. trisulcata* in the Yale Peabody Museum collections; the syntypes of *L. trisulcata* var. *blanda,* referred to above; and 11 Recent valves, representing six individuals, of *L. trisul-*

*cata,* labeled only "West Indies" in the National Museum of Natural History collection. The types of *P. (C.) recurrens, P. (C.) trisulcatus* var. *whitfieldi, P. (C.) parawhitfieldi, P. (C.) prunus,* and *P. (C.) multistriatus* Mansfield *non* Conrad were subsequently examined.

*Discussion.* — An attempt to resolve the nomenclatural problems associated with the species *L. trisulcata* is an excellent example of the difficulty of subdividing a continuously evolving lineage. Specific names have been proposed for distinctive morphological variants, for geographically separated entities, and for groups of specimens of different geological ages. There is a great deal of morphological variation, particularly in shape and in surface sculpture, within this lineage, but no phylogenetic trends can be traced using these characters. Rather, the amount and kind of morphological variation which can be seen in the Miocene representatives of *L. (Cavilinga) trisulcata* are nearly the same as for the Recent specimens referred to this species.

Because some of the nomenclatural problems seem to result from misconceptions about what Conrad meant to include in *L. trisulcata,* I shall quote his original descriptions here. Also, Plate 28, figure 6, is a reproduction of his illustration of this species. Unfortunately, his type specimens have evidently been lost. His first description (Conrad, 1841) follows:

> *Lucina trisulcata.* Obovate, convex; with concentric lines, and two or three distinct concentric furrows; lunule profound. Differs from *L. alveata* of the lower tertiary in being less ventricose, and in the much more profoundly impressed lunule; the cardinal teeth are also very different.

An expanded and somewhat modified version of this description appeared four years later (Conrad, 1845), when the species was first figured. That description is quoted below:

> *Lucina trisulcata* — Plate 40, Fig. 5.
>
> Ovate, convex, elevated, with 2 or 3 remote concentric furrows and numerous concentric lines; anterior side rather longer than the posterior; posterior margin subtruncated; beaks prominent; lunule cordate and very profound; inner margin crenulated; cardinal and lateral teeth distinct.
>
> Con. Silliman's Journ., xli, p. 346.
>
> Loc. Natural well, Duplin Co., and Neuse river, N.C.

Conrad's locality data define the type horizon of this species as the Duplin Marl (uppermost Miocene). Fossil specimens subsequently collected from the Pliocene Waccamaw Formation of South Carolina (Tuomey and Holmes, 1857); the "post-Pliocene" of South Carolina (Holmes, 1860); and the Miocene of New Jersey (Whitfield, 1894) were identified with *L. trisulcata.* Both Holmes and Whitfield noted certain differences between their specimens and those described by Conrad. Holmes pointed out that many of his specimens lacked "concentric furrows" (growth rings). Whitfield, who had only two specimens of *L. trisulcata,* noted that they were flatter, with coarser concentric sculpture, a smaller and shallower lunule, and less prominent teeth, than specimens from North Carolina; one of the New Jersey specimens entirely lacked "concentric furrows". The exact age of Whitfield's collection, from a well at Atlantic City, apparently has not been determined; the Kirkwood Formation of this area is middle Miocene in age (Richards, 1967).

Dall's first proposal of the varietal name *blandus* occurred in a description (Dall, 1901b) of Recent American specimens of *"Phacoides (Cavilucina) trisulcatus* Conrad, 1841". He defined this species as "notable for its obliquity and its two or three strongly marked resting stages, from which the name is derived". Noting that Conrad's *Lucina trisulcata* was a Miocene fossil, Dall added:

> The recent shell usually called by this name is often very similar to the fossil, but there is a larger, flatter, less coarsely sculptured form in the West Indies, which has much less emphatic resting stages, and, if not distinct, is at least a recognizable variety, which may be called *blandus.* . . . It varies from white, through yellow, to orange color.

A more complete description, which contradicts the first in some details, is that in Dall and Simpson (1901). This description had evidently been prepared when the first appeared but was published later. The second description stated that *blandus* was "obliquely subtriangular, higher than long, with the beaks placed behind the center", with a deep lunule, short ligament, and "shallow radial furrow on the posterior slope". The surface was "finely concentrically ridged, also with three or four deeper sulci". There were two cardinals in each valve, with anterior and posterior laterals single in the right valve and double in the left. The color was "white, yellowish, or salmon". Dimensions were "length, 12; height, 13; diameter, 8 mm". Dall also noted that "the deep sulci, usually three in number, seem to indicate resting stages. The typical *trisulcatus* is a Miocene fossil." The specimen figured in Plate 28, figure 14, of this paper corresponds to Dall's second description of *blandus.*

It should be noted that in his second description Dall considered the presence of growth rings or resting stages characteristic of the variety *blandus,* though in the first he had stated that they tended to be "much less emphatic" on *blandus* than on *trisulcatus s. s.* At that time taxonomists used the word "variety" interchangeably for geographically defined subspecies and for striking individual variants. Apparently Dall meant to use it in the latter sense. He evidently did not intend to use the name *blandus* for all the living forms of the group, reserving *trisulcata* for the fossil forms, as some authors have done.

Blackwelder (1972) argued on a statistical analysis of over 300 shells, that *L. trisulcata* and *L. blanda* should be regarded as distinct species.

Dall (1903) recognized three fossil varieties, based on morphology and on geographic and stratigraphic distribution, of *L. trisulcata.* He restricted *L. trisulcata* var. *trisulcata* to small shells with "pronounced and numerous resting stages", occurring in the Duplin Marl (late Miocene), North Carolina; in the Caloosahatchee Formation (Pliocene), Florida; and, questionably, in the Recent. He placed Whitfield's (1894) New Jersey forms in a new variety, *whitfieldi,* which he also reported from the Oak Grove Sand (middle Miocene) of Florida and the Waccamaw Formation (Pliocene) of South Carolina. Finally, he reduced *L. multistriata* Conrad, 1843, whose type locality is the same as that of *L. trisulcata,* to the status of a variety of *trisulcata.* As previously stated, *L. multistriata* is probably a *Parvilucina;* Dall may, however, have based his conclusions on specimens not conspecific with Conrad's *multistriata.* Dall described the variety *multistriata* as having "feeble and obsolete radial striation and the general form of variety *Whitfieldi*".

After describing these varieties, Dall gave the following excellent summary of the taxonomic problems posed by *L. trisulcata*:

> Were the characters of these shells at all constant they would properly be regarded as species, but they appear to vary exceedingly, and analogous variation, quite as marked, may be observed in a sufficiently extended geographic series of the recent shell which goes under Conrad's name. I confess that I am unable to separate the various forms from each other specifically, and am obliged to regard them as mutations of an extremely variable polymorphic species.

Two other species described by Dall (1903) may be conspecific with *L. trisulcata. L. (C.) recurrens* is found in the Bowden Formation of Jamaica and the Alum Bluff Group and Tampa Limestone of Florida. Dall stated that this species more closely resembles *L. blanda* than do the forms he placed in *L. trisulcata.* The name *recurrens* reflects Dall's belief that the species was Oligocene in age and thus older than the "intervening" Miocene varieties of *trisulcata;* however, the Bowden and Alum Bluff are now considered middle Miocene in age and the Tampa, early Miocene. *L. (C.) recurrens* is thus partly contemporaneous with *L. trisulcata* and, I believe, synonymous with it.

A species from the middle Miocene Calvert Formation and St. Marys Formation of Maryland, originally described as *Phacoides (Parvilucina) prunus* Dall, 1903, was placed by Chavan (1937) in *Cavilinga.* Like Whitfield's New Jersey forms referred to *L. trisulcata,* it lacks growth rings; but the musculature, dentition, and strong anterior expansion all indicate affinity with *Cavilinga.* Glenn (1904) recorded both *L. (C.) trisulcata* and *L. (C.) pruna* from the middle Miocene of Maryland. Mansfield (1932) suggested that Glenn's specimens of *trisulcata* should have been placed in *pruna.* Conversely, I have synonymized *pruna* with *trisulcata.* The middle Miocene (Calvert Formation) specimens in the Yale Peabody Museum collections closely resemble those figured by Glenn. Comparison of these (Pl. 28, figs. 10-12) with the Recent individuals (Pl. 28, figs. 7-9; Pl. 29, figs. 13-15) and with the figure of Conrad's specimen (Pl. 28, fig. 6) will demonstrate the great morphological variation with *L. (C.) trisulcata;* yet all these forms are connected by morphological and stratigraphic intermediates.

Gardner (1926) introduced the name *parawhitfieldi* for the Florida individuals which Dall had placed in *L. (C.) trisulcata* var. *whitfieldi.* She also recorded *trisulcata s. s.* from the Alum Bluff Group, but her only figures of it were reproductions of those in Glenn (1904). Her statement that "numerous strongly defined resting stages are absent in *trisulcata s. s.*" is not borne out by Conrad's descriptions and figures.

I examined the specimens which Mansfield (1932) and Gardner (1944) figured as *L. trisulcata multistriata* and believe them to be conspecific with *L. trisulcata* Conrad, not with *L. multistriata* Conrad. (Mansfield's specimens are USNM 371181, from the late Miocene Choctawhatchee Formation of Florida; Gardner's is USNM 325538, from the Pliocene Waccamaw Formation of North Carolina.)

The presence or absence of concentric growth rings has been used as a character differentiating species of *Cavilinga.* Chavan, in fact, cited as one of the characters defining this subgenus "des arrêts dans l'accroissement, marqués par plusieurs abrupts très nets de la surface externe" (Chavan, 1937, p. 198). Examining the biological significance of these structures thus may be informative. Shells of many species of bivalves, particularly those from areas with distinct winter and summer seasons, show well-marked rings which record temporary cessation of the growth of the shell. Growth usually slows down or stops during colder weather. It may also be interrupted, producing a ring, if the animal is disturbed. Seasonal growth rings mark off the shell into subequal intervals.

Craig and Hallam (1963) measured the distance from the umbo to each growth ring on about 2900 individuals of *Cardium edule* from Scotland. They chose an infaunal species and measured a large number of shells to minimize the influence of disturbance rings on the data, since seasonal and disturbance rings ordinarily cannot be told apart. Plotting frequency against distance from the umbo, they obtained a histogram with three well-defined peaks, whose modal values occurred at distances of 6, 15, and 26 mm from the umbo. Such a pattern reflects reproduction at only one time during the year, with the young all growing at about the same rate until a temporary halt in growth is produced with the onset of cold winter temperatures. Thus all individuals of the same age would have growth rings developed at about the same positions on the shell.

Craig (1967) extended the study to tropical species. Four of those which he studied in the Bahamas are lucinids [*L. (Lucina) pensylvanica, C. (Codakia) orbicularis, A. (Anodontia) alba,* and *Divaricella (Divalinga) quadrisulcata*]. He found that growth rings in tropical species show no consistent pattern of peaking like that shown by *Cardium edule.* This observation could be accounted for in two ways: either there is no seasonality in reproduction in these species, young being added to the population throughout the year; or there is no cessation of growth in the winter, and the rings formed reflect only events unique to each individual. Both factors could be acting simultaneously, or one could be operating for some species and the second for others.

Most of the lucinid species included in the present study tend to have growth rings developed at different distances from the umbo in different individuals (though my sample sizes are much smaller than those of Craig and Hallam and of Craig, and thus the irregular development of growth rings in most species of Lucinidae cannot be considered rigorously established). In some species growth rings were altogether lacking or seen on only one or two of the individuals examined; these species are usually those with both radial and concentric sculpture, or with two orders of concentric ribs. When growth rings are developed, they are usually only ill-defined irregularities in the shell surface (cf. Pl. 35, fig. 4). In contrast, in most individuals of the species here placed in *Cavilinga,* as well as of a few other species [e. g., *Divaricella (Egracina) dentata*], the growth rings are deeply impressed and divide the surface into approximately equal intervals (cf. Pl. 28, fig. 9).

The growth rings of these lucinid species apparently do not result from seasonal cessation of growth. In the *L. (Cavilinga) trisulcata* complex, growth rings are generally absent on individuals from the northern part of the range of the group but are present on approximately contemporaneous related individuals from southern localities. (In the Miocene, they are absent or rare on *L. trisulcata* "var." *whitfieldi* from New Jersey and *L. t.* "var." *pruna* from Maryland, but present on *L. t. trisulcata* from North Carolina and *L. t. recurrens* from Jamaica.) *L. (C.) pomilia,* from the Gosport Sand of Alabama, generally has well-defined growth rings; but the name *L. (C.) smithi* has been used for some individuals from this sand which look exactly like *pomilia* except that they lack growth rings. Also common in the Gosport Sand is *L. (Callucina?) papyracea,* on which growth rings are irregularly spaced and inconspicuous. Similarly, *Divaricella (Divalinga) quadrisulcata* and *D. (Egracina) dentata* both live in tropical regions, but one of the characters distinguishing them is the tendency of *D. (E.) dentata* to have regularly spaced growth rings.

Possibly the lucinid species which have well-developed growth rings have a tendency toward seasonal reproduction; the rule in most lucinids, conversely, may be continuous recruitment and continuous growth, with cessations of growth caused only by disturbances. In some species shell growth may stop during reproduction (Craig and Hallam, 1963), and perhaps this occurred only in the warm-water representatives of *L. (C.) trisulcata* in the Miocene.

### **Lucina (Cavilinga) pomilia** Conrad

Plate 28, figures 16-20

*Lucina pomilia* Conrad, 1833c, p. 40; Conrad, 1846b, p. 402, pl. 4, fig. 17; Harris, 1897, pp. 70-71, pl. 14, fig. 3, a, b; Harris, 1919, pp. 115-116, pl. 37, figs. 27-29 [not *L. carinifera* Conrad], pl. 38, figs. 6-11; Stewart, 1930, p. 178; E. J. Moore, 1962, p. 88.
*Phacoides (Here) pomilius* (Conrad), Dall, 1903, p. 1364.
*Linga (Cavilinga) pomilia* (Conrad), Chavan, 1937, pp. 148-151, 200; Chavan, 1938, p. 217; Palmer and Brann, 1965, pp. 174-175.
*Lucina impressa* Lea, 1833, p. 37, pl. 1, fig. 30.
*Lucina alveata* Conrad, 1833c, p. 40; Conrad, 1846b, p. 402, pl. 4, fig. 12; E. J. Moore, 1962, p. 37.
*Phacoides (Cavilucina) alveatus* (Conrad), Dall, 1903, p. 1364.
*Lucina pomilia* var. *alveata* Conrad, Harris, 1919, pp. 115-116, pl. 38, figs. 12-17.
*Linga (Cavilinga) pomilia* var. *alveata* (Conrad), Chavan, 1937, p. 200; Chavan, 1938, p. 217.
*Linga (Cavilinga) pomilia alveata* (Conrad), Palmer and Brann, 1965, p. 175.
*Lucina lunata* Lea, 1833, p. 58, pl. 1, fig. 32.
*Lucina smithi* Meyer, 1886, p. 81, pl. 1, fig. 23.
*Lucina pomilia* var. *smithi* Meyer, Harris, 1919, pp. 114-115, pl. 38, figs. 1-5.
*Phacoides (Parvilucina) smithi* (Meyer), Dall, 1903, p. 1381 [part].
*Linga (Cavilinga) smithi* (Meyer), Chavan, 1937, p. 200; Palmer and Brann, 1965, p. 175.

*Description.* — Shell of very small size (median length of 26 specimens 5.8 mm, range 4.6-8.0 mm), shape extremely variable (median H/L of 33 specimens 1.03, range 0.87-1.16), strongly inflated (median D/L of 26 specimens 0.40, range 0.30-0.49), anterior expansion moderate to great (median A/L of 33 specimens 0.50, range 0.37-0.59). Surface sculpture concentric, distinct to coarse; growth rings varying in number from none to eight, most commonly three or four; when two or more are present, usually deeply impressed and regularly spaced. Dorsal areas faint, anterior one forming pseudo-lunule. Lunule, ligament, and musculature as in *Lucina (Cavilinga) trisulcata.* Hinge plate relatively wider and beaks more elevated than in *L. (C.) trisulcata.* Anterior and posterior cardinals single in right valve, double in left; two cardinals in each valve; cardinals in right valve approximately equal in size, posterior one bifid; pallial blood vessel scar present; inner ventral margin denticulate.

*Types.* — The type specimens of *L. (Cavilinga) pomilia* and *L. (C.) alveata* Conrad are in the Academy of Natural Sciences of Philadelphia. *L. (C.) pomilia* is represented by four probable syntypes, ANSP 30524; and *L. (C.) alveata* by seven probable syntypes, ANSP 30510 (E. J. Moore, 1962). Nine specimens in the Philadelphia Academy, ANSP 5155-5163, are the probable syntypes of Lea's *Lucina impressa;* I was unable to find his types of *L. lunata.* The holotype of *Lucina smithi* Meyer, a right valve, is in the U.S. National Museum of Natural History (USNM 1357).

*Material.* — The phenetic study was based on about 75 specimens in the collections of the Yale Peabody Museum, all from the upper middle Eocene Gosport Sand of Alabama. The type specimens listed above were subsequently examined, as were the early and middle Eocene specimens from Alabama figured by Harris (1897, 1919), which are in the Paleontological Research Institution.

*Discussion.* — Several specific names have been proposed for striking variants of this species, but in material collected from the same locality these variants can be seen to intergrade completely. Conrad's name *pomilia* was proposed for specimens approximately equal in height and length, moderately to strongly inflated, with a moderate anterior expansion and two to four deep, regularly spaced growth rings (Pl. 28, fig. 16). The name *alveata* referred to individuals which are higher than long, with A/L more than 50%; the dorsoventral elongation and anterior expansion produce a triangular shape; growth rings are generally more numerous than in *pomilia,* and inflation is greater (Pl. 28, fig. 17). Meyer's (1886) name *smithi* was based on specimens with the same shape as *pomilia,* or more elongated anteroposteriorly, having coarser concentrics than *pomilia* and *alveata,* and having no growth rings or only one or two near the ventral margin (Pl. 28, fig. 19). These individuals are almost indistinguishable from the middle Miocene representatives of *L. (C.) trisulcata* from Maryland (Pl. 28, fig. 10). Harris (1919) was the first to point out the intergradation between the three Eocene forms and to treat all as variants of a single species. It should be noted that, though Conrad's name *alveata* has page precedence over his *pomilia,* Harris as the first reviser subordinated *alveata* to *pomilia* [see International Code of Zoological Nomenclature, 1964, Art. 24(a)].

Dall (1903) and Harris (1897, 1919) synonymized Lea's *Lucina impressa* and *L. lunata* with Conrad's *L. pomilia* and *L. alveata,* respectively. Conrad's brief descriptions, unaccompanied by figures, of specimens from the Eocene of Alabama have priority by a few months over Lea's more detailed, illustrated work dealing with the same species. Wheeler (1935) explained the origin of this situation. A resident of Claiborne, Alabama, had sent a shipment of fossil shells to the Academy of Natural Sciences of Philadelphia, with which Lea was affiliated. Lea apparently having indicated that he did not have time to describe the Claiborne fauna, Conrad, who had recently completed two numbers of a work on the Tertiary fossil shells of North America, was appointed by the members of the Philadelphia Academy to make further collections in Alabama and describe the species. While Conrad was in Alabama, however, Lea decided to describe the shipment of Claiborne fossils. Conrad, advised of Lea's intentions, hurriedly gave names to the Alabama species, wrote brief descriptions, and sent them to friends in Philadelphia (S. G. Morton and Thomas Say), who prepared his manuscript for publication. It appeared as Numbers 3 (September, 1833) and 4 (November, 1833) of *Fossil Shells of the Tertiary Formations of North America.* Just prior to the publication of Conrad's third number of *Fossil Shells,* Lea had read a paper describing the fossils to the Philadelphia Academy. His descriptions, however, published as part of a work entitled *Contributions to Geology,* did not appear in print until December, 1833. Conrad's names thus have clear priority. Though some authors have suggested rejecting his names for the Alabama Eocene species because of the sketchiness of his descriptions, most of his type specimens are still in existence at the Philadelphia Academy, and there is no reason for considering his species unidentifiable.

### **Lucina (Cavilinga) lingualis** Carpenter

Plate 29, figures 1-3

*Lucina lingualis* Carpenter, 1864a, p. 313.
*Phacoides (Cavilucina) lingualis* (Carpenter), Dall, 1901b, pp. 811, 827, pl. 39, fig. 7; Lamy, 1920, p. 207.
*Lucina (Myrtea) lingualis* Carpenter, Grant and Gale, 1931, p. 286.
*Lucina (Callucina) ligualis* [error] Carpenter, Chavan, 1937, p. 254.
*Lucina (Cavilinga) lingualis* Carpenter, Hertlein and Strong, 1946, p. 113; Palmer, 1963, pp. 304-305, pl. 59, figs. 1-5.
*Lucina (Cardiolucina) lingualis* Carpenter, Durham, 1950, p. 76, pl. 18, figs. 3, 10.
*Lucina (Callucina) lingualis* Carpenter, Keen, 1958, p. 94, fig. 186.
*Lucina (Cavilinga) linqualis* [error] Carpenter, Olsson, 1961, p. 211, pl. 31, fig. 11.
? *Lucina prolongata* Carpenter, 1857, pp. 100-101; Brann, 1966, pl. 12, fig. 145.
? *Phacoides (Cavilucina) prolongatus* (Carpenter), Dall, 1901b, p. 811; Lamy, 1920, p. 207.
? *Linga (Cavilinga) prolongata* (Carpenter), Chavan, 1937, p. 201.
? *Lucina (Cavilinga) prolongata* Carpenter, Keen, 1958, p. 94, fig. 187; Olsson, 1961, pp. 210-211, pl. 31, figs. 8, 8a, 10-10b; Keen, 1968, p. 396, pl. 56, figs. 22 a-d types.

*Description.* — Shell of small size (median length of 24 specimens 11 mm, range 9-18 mm), higher than long (median H/L 1.05, range 0.99-1.12), moderately inflated (median D/L 0.29, range 0.22-0.31), anterior expansion moderate to great (median A/L 0.52, range 0.44-0.60). Surface sculpture concentric, with growth rings deep, usually regularly spaced. Dorsal areas faint. Lunule deep, short, wide, triangular, slightly asymmetrical. Ligament external. Anterior adductor scar of normal length and width, curved away from pallial line; posterior adductor scar elliptical; pedal retractor musculature as in *L. (C.) trisulcata.* Hinge plate narrow, with anterior and posterior laterals single in right valve, double in left; posterior laterals often obsolescent. Two cardinals in left valve; one, slightly bifid, in right. Shell exterior usually white, sometimes tinged with pink or orange; shell interior generally pink or orange. Pallial blood vessel scar present; inner ventral margin finely denticulate.

*Types.* — Palmer (1963) listed the locations of the types of species described by Carpenter from the west coast of Mexico and Panama, excluding those of the Mazatlán Collection [see discussion of *L. (Parvilucina) tenuisculpta*]. Carpenter deposited duplicate sets of a number of his species at two or more of the museums with which he was associated. Palmer found that six syntypes of *Lucina lingualis* had been deposited in the National Museum of Natural History (USNM 15898) and three in the Redpath Museum, McGill University, Montreal (Redpath Mus. No. 114). Palmer figured the three Redpath Museum and one of the National Museum specimens (Palmer, 1963, pl. 59, figs. 1-5). The original specimens of *Lucina prolongata,* here tentatively synonymized with *L. (C.) lingualis,* are part of the Mazatlán Collection in the British Museum (Natural History) (Keen, 1968, p. 396, pl. 56) [see discussion of types of *L. (Here) excavata* Carpenter].

*Material.* — The phenetic study was based on about 30 Recent specimens, all from Baja California or the Gulf of California, in the collections of the Yale Peabody Museum and the National Museum of Natural History; the National Museum material included Carpenter's syntypes of *L. (C.) lingualis.*

*Discussion.* — Dall (1901b) considered this species the Pacific analogue of *Lucina trisulcata* Conrad. When Chavan (1937) proposed the new subgenus *Cavilinga* with *L. trisulcata* as its type, he excluded *L. lingualis* and *L. lampra* (Dall, 1901b), placing them in *Callucina.* He based this exclusion on unspecified "differences in the hinge line", stating also that the growth rings in *Cavilinga* were more numerous and better marked than in *L. lingualis* and *L. lampra,* and that the size of adults of *Cavilinga* was always much less than that of adults of *Callucina.* These supposed differences are based on misconceptions. Though the posterior laterals are reduced in some individuals of *L. lingualis* and *L. lampra,* the anterior laterals are well developed. As shown in the discussion of *L. trisulcata,* the development of growth rings may vary considerably within a species, even among individuals from the same locality. Specimens of *L. trisulcata* "var. *blanda*", *L. lingualis*, and *L. lampra* are about equal in size. Also, the two latter species, like *L. trisulcata,* have only concentric sculpture; they lack the radial sculpture which is characteristic of the Late Tertiary species of Callucina. The similarity between *L. lingualis* and Dall's figured syntype of *L. trisulcata* "var. *blanda*" is particularly striking (cf. Pl. 28, figure 13, and Pl. 29, figure 1).

*Lucina prolongata* Carpenter, smaller in size and with a stronger anterior expansion than *L. (C.) lingualis,* may be the juvenile of it. Many lucinids show allometric changes with growth in anterior expansion, the anterior of the shell being proportionately longer in younger specimens.

### **Lucina (Cavilinga) lampra** (Dall)

Plate 29, figures 4-6

*Phacoides (Cavilucina) lamprus* Dall, 1901b, pp. 808, 811, 827, pl. 39, fig. 9; Lamy, 1920, p. 208.
*Lucina (Callucina) lampros* [error] (Dall), Chavan, 1937, p. 252.
*Lucina (Cardiolucina?) lampra* (Dall), Durham, 1950, p. 76, pl. 18, figs. 1, 9.
*Lucina (Callucina) lampra* (Dall), Keen, 1958, p. 94, fig. 185.
*Lucina (Cavilinga) lampra* (Dall), Olsson, 1961, p. 211, pl. 31, fig. 12.

*Description.* — Shell small (median length of 23 specimens 17 mm, range 11-21 mm), somewhat longer than high (median H/L 0.95, range 0.88-0.97), moderately inflated (median D/L 0.25, range 0.18-0.28), anterior expansion moderate to great (median A/L 0.47, range 0.36-0.55). In all other respects closely similar to *L. (Cavilinga) lingualis.*

*Types.* — The specimen figured by Dall is in the National Museum of Natural History type collection (USNM 41626); the type locality is La Paz, Baja California.

*Material.* — The phenetic study was based on about 25 Recent specimens, all from Baja California or the Gulf of California, in the collections of the Yale Peabody Museum; and on Dall's holotype.

*Discussion.* — Taxonomic differentiation between this species and the preceding seems to have been based almost exclusively on the fact that *L. lingualis* is higher than long and *L. lampra* longer than high. *L. lampra* seems to average slightly larger and to show a less strong anterior expansion (two characters which tend to be correlated with age). There is no evidence that the two species are reproductively isolated from each other or have different ecological preferences.

I retain the traditional specific assignments here, however, because investigation of this interesting taxonomic problem was beyond the scope of this study. As further evidence for the placement of *L. lampra* and *L. lingualis* in *Cavilinga*, it may be noted that Dall (1901b, p. 808) considered *L. trisulcata* "var. *blanda*" to be "intermediate between the typical [*Phacoides*] *trisulcatus* and the Pacific Coast *P. lamprus*".

### Subgenus **BELLUCINA**

*Author.* — Dall, 1901b, p. 806.

*Type species.* — *Parvilucina eucosmia* Dall, 1901b (new name for *Lucina pisum* Reeve, 1850, *non* Sowerby, J. de C., 1837) (= *Lucina semperiana* Issel, 1869, *fide* Lamy, 1920), by original designation.

*Discussion.* — Dall (1901b) proposed *Bellucina* as a section of *Parvilucina,* one of his subgenera of *Phacoides.* In addition to the type, a Recent Indo-Pacific species whose range Lamy (1920) gave as from the Red Sea to the Philippines, Dall included two other Recent species: the West Atlantic and Caribbean *Phacoides (Bellucina) amiantus* Dall, 1901b (a new name for *Lucina costata* Holmes *non* d'Orbigny), and *Lucina cancellaris* Philippi, 1846, found from Baja California to Panama.

Chavan (1937) did not consider the latter two species congeneric with the type. I have not seen specimens of the type species. From Reeve's figures (Reeve, 1850, pl. 11, figs. 66a, b), it is a small, rounded shell with conspicuous dorsal areas and with concentric and radial sculpture, the radial ribs being about 20 in number and approximately equal in prominence to the concentrics. In *L. amiantus* and *L. cancellaris,* however, the number of radials is about 8 to 12, and the radials are definitely more prominent than the concentrics. Chavan (1937) placed these species in *Pleurolucina,* but I disagree with this assignment for reasons which will be given in the discussion of that subgenus. If the type species of *Bellucina* is a *Parvilucina,* a new subgeneric name will have to be proposed for the distinctive group of species to which *L. amiantus* belongs.

Britton (1972) proposed a new subgenus *Radiolucina* with *Phacoides (Bellucina) amiantus* Dall, 1901b, type species.

Chavan (1937) synonymized *Cardiolucina* Sacco, 1901 (which Gardner and others used as approximately equivalent to Chavan's *Cavilinga*), with *Bellucina.* He believed that the type of *Cardiolucina, Cardium agassizi* Michelotti, 1847, was congeneric with *L. (Bellucina) semperiana.* Judging only from Sacco's photographs, which admittedly are not good, this hypothesis seems untenable. At any rate, *Cardiolucina* (June, 1901) was proposed before *Bellucina* (August 22, 1901), though Chavan used the latter name for the taxon. The dates of Sacco's 30-volume work, Part 29 of which includes the Lucinidae, are given in his Part 30. Keen (1958) listed the dates of Dall's works.

The ensuing diagnosis of *Bellucina* includes the North American species, the only ones which I have been able to examine. It is unfortunate that Dall did not designate one of these as type of *Bellucina,* particularly considering the brevity and ambiguity of his description of the group. After describing the subgenus *Parvilucina* ("Shell small, more or less inequilateral, sculpture more or less reticulate but not muricate, teeth small, but all usually present"), Dall divided it into two sections, *Parvilucina s. s.* ("Dorsal areas obscure or obsolete, sculpture feeble") and *Bellucina* ("Dorsal areas and sculpture strong").

*Diagnosis.* — Shell of very small to small size, shape varying from longer than high to higher than long, moderately to strongly inflated, anterior expansion moderate to great. Surface sculpture concentric and radial; radial sculpture dominant, generally of 8-12 broad, flat radial ribs, with small secondary ribs sometimes occurring in interspaces between primary radials; less commonly of about 15-20 radials, all of equal size. Growth rings either absent or developed only near ventral margin. Anterior dorsal area distinct, forming pseudo-lunule; posterior dorsal area conspicuous, set off by virtual absence of radial sculpture; small elevated spines present along posterior dorsal margin. Lunule short, wide, deep, triangular, slightly asymmetrical. Anterior adductor scar of normal length and width, straight, parallel to pallial line; posterior adductor scar round or elliptical; anterior pedal retractor scar separate from anterior adductor, but posterior pedal retractor not evident. Hinge plate wide; anterior and posterior laterals single in right valve, double in left; two cardinals in each valve, but right anterior cardinal reduced; right posterior cardinal strongly bifid. Pallial blood vessel scar present; inner ventral margin denticulate.

*Distribution and phylogenetic relationships.* — In addition to the three Recent species whose habitats are given above in the discussion of the name *Bellucina,* Lamy (1920) included in the subgenus the species *Lucina rugosa* Hedley, 1909, from China and Australia; and *L. lamothei* Dautzenberg, 1912, from Portuguese Guinea. *Bellucina* is thus one of the more widely distributed subgenera of *Lucina.*

Grant and Gale (1931) listed *L. (Bellucina) cancellaris* as occurring in lower Pleistocene strata of Baja California. *L. (B.) waccamawensis* (Dall, 1903), named for its occurence in the Pliocene Waccamaw Formation of South Carolina, is also common in the Pliocene Caloosahatchee

Marl of Florida (DuBar, 1958); it is practically indistinguishable from the Recent *L. (B.) amiantus*. Also closely similar to *amiantus* is *L. (B.) katherinepalmerae* Weisbord, 1964, from the Pliocene Mare Formation of Venezuela.

*L. (B.) tuomeyi* (Dall, 1903), from the late Miocene Duplin Marl of North Carolina and South Carolina and Choctawhatchee Formation of Florida (Mansfield, 1932), differs from *L. (B.) waccamawensis* in having one or two fewer radial ribs than the Pliocene species; also, the interspaces between the ribs are shallow, so that the shell surface lacks the undulatory character seen in *amiantus, cancellaris,* and *waccamawensis.* The radials of *tuomeyi* tend to become inconspicuous ventrally and toward the center of the shell, as do those of species of *Callucina.*

Two middle Miocene species which seem unquestionably to belong to this subgenus are *L. (B.) nereidedita* (Maury, 1910) and *L. (B.) euphaea* (Gardner, 1926), both from the Alum Bluff Group of Florida. (They may be conspecific.) They are more similar to the Recent *L. (B.) amiantus* than to the late Miocene *L. (B.) tuomeyi.* The earliest North American *Bellucina, L. (B.) tampaensis* (Dall, 1915), from the early Miocene Tampa Limestone of Florida, closely resembles *L. (B.) euphaea.*

Dall (1903) described *Phacoides (Bellucina) actinus* from the middle Miocene Bowden Formation of Jamaica; he believed this species to represent a transition between *Parvilucina* and *Bellucina.* Its phylogenetic significance to him was bolstered by his belief that the Bowden was Oligocene in age; still, morphologically if not stratigraphically it is a good intermediate between the two subgenera. It has been mentioned briefly in the discussion of *Parvilucina.* Externally, it closely resembles *L. (P.) sphaeriola,* the abundant *Parvilucina* of the Alum Bluff Group, except that *sphaeriola* generally has about 24 radial ribs and *actina* only about 18; also, the radials are more prominent relative to the concentrics in *actina.* Internally, the two species can be distinguished by the anterior adductor scar, which is short and curved in *sphaeriola,* longer and straight in *actina.* Of all the North American species which Dall placed in *Bellucina, L. (B.) actina* is the one most closely resembling Reeve's figures of the type species.

Chavan (1937) assigned one middle Eocene European species, *Phacoides (Parvilucina) ligatus* Cossmann and Pissarro, 1904, to *Bellucina.* Again, it should be noted that Chavan's concept of *Bellucina* is somewhat different from Dall's which is accepted here. Species similar to *L. (B.) amiantus* do not seem to have been recorded prior to early Miocene time. Chavan's placement of Cossmann and Pissarro's species in *Bellucina* may, in fact, be a further indication of a close relationship between *Bellucina* and *Parvilucina.*

### **Lucina (Bellucina) amiantus** (Dall)

Plate 29, figures 7-10

*Lucina costata* Holmes, 1860, p. 28, pl. 6, fig. 2; Dall, 1889, p. 50 [*non L. costata* d'Orbigny, 1846, p. 586, *nec L. costata* Tuomey and Holmes, 1857, p. 60, pl. 18, figs. 12, 13].
*Phacoides (Bellucina) amiantus* Dall, 1901b, pp. 810, 826-827, pl. 39, fig. 10; Lamy, 1920, p. 216.
*Linga (Pleurolucina) amiantus* (Dall), Chavan, 1937, p. 214.
*Lucina (Bellucina) amiantus* (Dall), Abbott, 1954, pp. 385-386, fig. 78c.
*Lucina amiantus* (Dall), Parker, 1960, pp. 317, 334, pl. 3, fig. 19a, b.
? *Lucina costata* Dall, 1892, p. 210 [? = *L. costata* Holmes, 1860].
? *Phacoides (Bellucina) waccamawensis* Dall, 1903, p. 1386, pl. 52, fig. 2; DuBar, 1958, p. 168, pl. 7, fig. 11.
? *Linga (Pleurolucina) waccamawensis* (Dall), Chavan, 1937, pp. 213-214.

*Description.* — Shell of very small size (median length of 18 specimens 5.4 mm, range 3.4-8.2 mm), elongate to round (median H/L of 22 specimens 0.92, range 0.88-1.01), moderately to strongly inflated (median D/L of 18 specimens 0.33, range 0.24-0.47), anterior expansion moderate to great (median A/L of 22 specimens 0.53, range 0.42-0.58). Change in degree of inflation during ontogeny is apparent: median D/L of 6 small (length less than 5 mm) specimens 0.27, range 0.24-0.29; median D/L of 12 larger specimens 0.38, range 0.28-0.47 (compare Pl. 29, fig. 7, and Pl. 29, fig. 8). Surface sculpture of 8 to 12 broad radial ribs crossed by threadlike concentric ribs; on small shells interspaces between radials are deep, giving shell a plicate or undulatory surface (Plate 29, figure 8); spaces between radials shallower on larger shells, radials thus becoming less distinct, particularly near center of shell (Plate 29, figure 7); small secondary radials sometimes occur in interspaces on ventral two-thirds of shell, giving impression of bifurcating radials. Concentric ribs all equally prominent; growth rings absent, except that on some larger shells one or two occur near ventral margin. Anterior dorsal area distinct, forming pseudo-lunule; posterior one conspicuous, lacks radials; row of spines formed along posterior dorsal margin by terminations of concentrics (Plate 29, figure 8). Lunule deep, short, wide, triangular, slightly asymmetrical. Ligament external. Anterior adductor scar of normal length and width, straight, closely parallel to pallial line. Posterior adductor scar round. Anterior pedal retractor scar separate from adductor scar; posterior one not evident. Hinge plate wide, with full complement of cardinal and lateral teeth, except that right anterior cardinal is reduced in size or partly effaced by the deep lunule. Pallial blood vessel scar present. Inner ventral margin fluted by termination of radial ribs and also finely denticulate.

*Types.* — The holotype of *L. (B.) amiantus* is in the

National Museum of Natural History (USNM 64276). The type locality is Yucatan Strait. The syntypes (four valves) of *L. (B.) waccamawensis,* here tentatively synonymized with *amiantus,* are also in the National Museum (USNM 157790). Although the name of this species is derived from the Waccamaw Formation (Pliocene) of South Carolina, according to the label the syntypes were collected from the Caloosahatchee Marl (Pliocene) of Florida. The original of *Lucina costata* of Holmes, 1860, is in the American Museum of Natural History, but the specimen which Tuomey and Holmes (1857) called *L. costata* is missing from that collection (Dr. N. D. Newell, written communication, 1971).

*Material.* — The phenetic study was based on about 25 Recent specimens, all from western Florida, in the collections of the Yale Peabody Museum. Dall's types of *L. amiantus* and *L. waccamawensis* were subsequently examined.

*Discussion.* — This species has been reported living throughout the Gulf of Mexico and in the western Atlantic from North Carolina to San Sebastian, Brazil (Dall, 1901b; Abbott, 1954; Parker, 1960). Its eastern Pacific analogue is *L. (B.) cancellaris* Philippi, 1846. *Bellucina* has not been reported in western North America from beds older than Pleistocene.

*L. (B.) amiantus* and the Pliocene *L. (B.) waccamawensis* are similar and are tentatively synonymized here. The species now named *L. (B.) amiantus* was called *Lucina costata* by Holmes (1860) and Dall (1889). The same name had previously been applied to two other species. *L. costata* d'Orbigny, 1846, is the species placed in *Ctena* by Dall and here assigned provisionally to *Parvilucina. L. costata* Tuomey and Holmes, 1857, was renamed *Phacoides (Bellucina) tuomeyi* by Dall (1903); its radial ribs are less prominent and less numerous than those of *L. (B.) amiantus. L. costata* of Dall, 1892, was renamed *P. (Bellucina) waccamawensis* by Dall (1903); as stated above, it and *L. (B.) amiantus* (and, thus, *L. costata* of Holmes, 1860, and Dall, 1889) are probably synonymous.

### Subgenus **LUCINISCA**

*Author.* — Dall, 1901b, p. 805.

*Type species.* — *Lucina nassula* Conrad, 1846a, pp. 24-25, by original designation.

*Discussion.* — Dall (1901b) proposed *Lucinisca* as a subgenus of *Phacoides.* Chavan (1937) expanded Dall's brief diagnosis of the subgenus.

*Diagnosis.* — Shell of small to large size, moderately elongate to round, flat to strongly inflated, anterior expansion moderate. Surface sculpture of both radial and concentric ribs; radials thinner and more numerous than in *Bellucina,* more prominent than in *Parvilucina;* concentrics varying in prominence from slightly stronger than radials to almost completely lacking. Development of nodes at intersections of concentrics and radials creates coarse surface; no growth rings. Dorsal areas distinct or conspicuous; anterior one may be set off by change in sculpture (crowding together of concentric ribs) or may form pseudo-lunule; posterior dorsal margin often bears spines at terminations of concentric ribs. Lunule shallow or deep, variable in size and shape. Ligament external. Anterior adductor scar of normal length and width, straight, parallel to pallial line; posterior adductor scar round. Anterior pedal retractor scar separate from adductor; posterior one partly separate in some species, not evident in others. Hinge plate narrow; anterior and posterior laterals single in right valve, double in left; one cardinal in right valve, two in left. Pallial blood vessel scar present. Inner ventral margin fluted by terminations of radial ribs, usually not denticulate.

*Distribution and phylogenetic relationships.* — *Lucinisca* is well represented in the Recent fauna. There are five Recent North American species: *L. (Lucinisca) nassula* Conrad, 1846a, and *L. (L.) muricata* (Spengler, 1798), from the southeastern United States and the Caribbean; and *L. (L.) nuttalli* Conrad, 1937; *L. (L.) fenestrata* Hinds, 1845; and *L. (L.) liana* (Pilsbry, 1931), from tropical West America. *L. (Lucinisca) muricata* and *L. (L.) fenestrata* are particularly interesting. The sculpture of *muricata* is almost exclusively radial: the nodal intersections between concentric and radial ribs have been transformed into sharp spines, the radial ribs are very strong, and the concentric ribs rarely persist across the interspaces between radials. Dall (1903) stated that he had seen no lucinid species in which only radial sculpture is present; *L. (L.) muricata* seems to be the only exception to his generalization. Stanley (1970) briefly discusses its ecology. It inhabits muddier substrata than do most nearshore lucinids, and the muricate sculpture may be an adaptation keeping the shell from sinking in the soft substratum. *L. (L.) fenestrata* is about twice as large as any of the other species of *Lucinisca;* Keen (1958) gave a height of 44 mm for a representative specimen. Because of its large size and radial sculpture, *L. fenestrata* externally resembles another West American species, *C. (Codakia) distinguenda.* Lamy (1920) listed one Recent Indo-Pacific species of *Lucinisca, L. (L.) venusta* Philippi, 1847. With this exception, *Lucinisca* seems to have been confined to the Western Hemisphere throughout its history (Chavan, 1937).

Both *L. (L.) nassula* and *L. (L.) nuttalli* are represented in the Pliocene and Pleistocene strata of their respective geographic areas (Dall, 1903; Grant and Gale, 1931). [A record of *L. nuttalli* from the late Miocene Santa Margarita Formation of California (Nomland, 1917) is not accompanied by a figure.] Weisbord (1964) also reported *L. (L.) muricata* from an unnamed clayey formation of probable late Pliocene age in Venezuela. Other Pliocene species of *Lucinisca* are *L. (L.) roigi* (Maury, 1925) which is closely similar to *L. (L.) muricata;* and *L. (L.) fausta* Pilsbry and Olsson, 1941, from the Canoa Formation of Ecuador, resembling *L. (L.) fenestrata.*

*Lucina (Lucinisca) cribraria* Say, 1824, from the late Miocene Yorktown Formation of Virginia and Choctawhatchee Formation of Florida (Gardner, 1944), closely resembles *L. (L.) nassula;* its concentric ribs tend to be discontinuous on the ventral third of the shell, also recalling the sculpture of *L. (L.) muricata.* Two species from the Gatun Formation of middle and late Miocene age on the Atlantic coast of Panama and Costa Rica, *L. (L.) costaricensis* and *L. (L.) bocasensis* (Olsson, 1922), resemble, respectively, *L. (L.) cribraria* and *L. (L.) nassula.*

Three species of *Lucinisca* have been named from the middle Miocene Alum Bluff Group of Florida. Both *L. (L.) plesiolopha* Dall, 1900, and *L. (L.) calhounensis* (Dall, 1903) have relatively less prominent radials and more prominent concentrics than do later species of *Lucinisca.* The surface sculpture of *L. (L.) plesiolopha* is most like that of *L. (L.) nassula,* but its long, triangular lunule is like that of *L. (L.) nuttalli.* I was unable to find the type of *L. (L.) calhounensis* in the National Museum of Natural History. From Dall's figure (1903, pl. 52, fig. 16), this species appears to resemble *Parvilucina* except for the greater prominence of its concentric ribs. I have no information about its musculature. Also, I have tentatively assigned to *Parvilucina* a species originally named *Codakia (Jagonia) chipolana* Dall, 1903; it externally resembles the Recent *L. (Parvilucina?) costata,* but its conspicuous posterior dorsal area and rounded posterior adductor scar are like those of species of *Lucinisca.*

Two early Miocene species of *Lucinisca* are known. *Lucina (Lucinisca) arrogans* Olsson, 1964, from the Angostura Formation of Ecuador, closely resembles *L. (L.) muricata. L. (L.) silicata* (Mansfield, 1937), like species of *Parvilucina,* has concentrics and radials which are about equally strong, and has faint dorsal areas. It, however, has only one cardinal in the right valve, and its anterior adductor scar is of normal length and straight; the posterior adductor scar is round, with the pedal retractor scar partly separate from it. The dentition and musculature of *silicata* thus suggest affinity with *Lucinisca.*

No Eocene or Oligocene species of *Lucinisca* have been recorded. Gardner (1935), however, assigned to *Lucinisca* a small species, *Phacoides (Lucinisca) mesakta,* from the Paleocene Midway Group of Texas. Closely similar to it is *Lucina linearia* Stephenson, 1941, from the Late Cretaceous (Maestrichtian) Navarro Group of Texas. These species are described and discussed under *Myrtea s. s.*

If these Upper Cretaceous and Paleocene species are excluded from it, *Lucinisca* evidently originated in late Oligocene or early Miocene time. Resemblances have been noted above between species of *Parvilucina* and some early and middle Miocene species probably belonging to *Lucinisca. Lucinisca* and *Bellucina* are also similar, especially in musculature and in the prominence of the dorsal areas. Probably both *Bellucina* and *Lucinisca* evolved from *Parvilucina* by increase in the coarseness of the surface sculpture and in the distinctness of the dorsal areas, with a concurrent increase in the length of the anterior adductor and change in shape of the posterior adductor (from elliptical to round).

### **Lucina (Lucinisca) nassula** Conrad

Plate 29, figures 11-14

*Lucina nassula* Conrad, 1846a, pp. 24-25.
*Phacoides (Lucinisca) nassula* (Conrad), Dall, 1901b, pp. 805, 808; Dall, 1903, p. 1372; Lamy, 1920, p. 184; Thiele, 1935, p. 866.
*Lucina (Lucinisca) nassula* (Conrad), Chavan, 1937, pp. 238, 240; Abbott, 1954, p. 388.
*Phacoides (Lucinisca) nassula* var. *caloosana* Dall, 1903, pp. 1372-1373.
*Lucina (Lucinisca) nassula caloosana* (Dall), Chavan, 1937, p. 240.
*Phacoides (Lucinisca) nassula caloosana* Dall, Olsson and Harbison, 1953, p. 88; DuBar, 1958, p. 169.

*Description.* — Shell of small size (median length of 23 specimens 10.3 mm, range 8.4-11.5 mm), slightly longer than high (median H/L 0.93, range 0.85-0.99), moderately to strongly inflated (median D/L 0.30, range 0.26-0.36), anterior expansion usually moderate (median A/L 0.48, range 0.41-0.56). Surface sculpture coarse; concentric sculpture dominant but radials well developed; concentrics all equally prominent, no growth rings. Dorsal areas conspicuous; anterior one forms pseudo-lunule; terminations of concentrics at posterior dorsal margin form spines. Lunule short, wide, triangular, slightly asymmetrical; in some individuals so short that it resembles "figure-8" lunule of small *Lucina pensylvanica.* Ligament external. Anterior adductor scar of normal length and width, straight, parallel to pallial line; posterior adductor scar round. Anterior pedal retractor scar separate from adductor; posterior pedal retractor not evident. Hinge plate narrow; anterior and posterior cardinals single in right valve, double in left; one cardinal (not bifid) in right valve, two in left. Pallial blood vessel scar present.

Inner ventral margin fluted by terminations of radial ribs, but not denticulate (Pl. 29, fig. 12).

*Types.* — If still extant, the original specimens of *Lucina nassula* Conrad are probably in the collections of the Department of Mollusks of the Academy of Natural Sciences of Philadelphia. The holotype of Dall's Pliocene "variety" *caloosana* is in the U.S. National Museum of Natural History (USNM 157824).

*Material.* — The phenetic study was based on about 35 Recent specimens, from Florida and Jamaica, in the collections of the Yale Peabody Museum. The holotype of *L. nassula* "var." *caloosana* was subsequently examined.

*Discussion.* — Abbott (1954) gave the distribution of this species as "North Carolina to Florida, Texas and the Bahamas". *L. nassula* "var." *caloosana* (Dall, 1903), from the Pliocene Caloosahatchee Marl of Florida, was described as the "immediate precursor" of the Recent form, differing in having more prominent concentric sculpture and a larger lunule. These differences seem, however, to be within the range of variation shown by Recent *L. nassula.*

### **Lucina (Lucinisca) nuttalli** Conrad

Plate 29, figures 15-18

*Lucina nuttallii* Conrad, 1837, p. 255, pl. 20, fig. 2.
*Phacoides (Lucinisca) nuttallii* (Conrad), Dall, 1901b, p. 812; Dall, 1903, p. 1373; Lamy, 1920, pp. 185-186.
*Lucina (Myrtea) nuttallii* Conrad, Grant and Gale, 1931, p. 288, pl. 14, figs. 4a, 4b, 18.
*Lucina (Lucinisca) nuttallii* Conrad, Chavan, 1937, p. 241; Keen, 1958, p. 96, fig. 191.
*Phacoides (Lucinisca) nuttalli* (Conrad), Abbott, 1954, p. 388, pl. 38g.
*Phacoides (Lucinisca) nuttallii* var. *centrifugus* Dall, 1901b, pp. 812, 828, pl. 39, fig. 13; Lamy, 1920, p. 186; Abbott, 1954, p. 389.
*Lucina (Lucinisca) nuttalli centrifuga* (Dall), Keen, 1958, p. 96.
*Phacoides nuttalli* var. *antecedens* Arnold, 1907, p. 436, pl. 55, fig. 6.

*Description.* — Shell of small to medium size (median length of 21 specimens 21 mm, range 15-25 mm), slightly elongate to round (median H/L 0.95, range 0.86-1.00), moderately inflated (median D/L 0.25, range 0.21-0.30), anterior expansion usually small to moderate (median A/L 0.45, range 0.37-0.52). Surface sculpture less coarse than in *L. nassula;* concentric ribs only slightly more prominent than radials, producing a cancellate sculpture; no growth rings. Dorsal areas conspicuous, both set off by change in sculpture; concentrics faint on anterior dorsal area; posterior dorsal area divided into two parts, with radial sculpture predominant near dorsal margin, concentric predominant near boundary between dorsal area and main part of shell (Pl. 29, fig. 15). Lunule long, narrow, triangular, more shallow than in *L. nassula,* slightly to strongly asymmetrical (greater part in left valve). Musculature as in *L. nassula,* except posterior pedal retractor scar evident in some individuals. Dentition as in *L. nassula,* with cardinal tooth in right valve slightly bifid; other internal features as in *L. nassula.*

*Types.* — Keen (1966) found two syntypes of *L. nuttalli,* one of which may be the figured specimen, in the Nuttall Collection of the British Museum (Natural History). Dall's (1901b) figured specimen of *L. nuttalli* var. *centrifuga* is in the National Museum of Natural History (USNM 108881). Arnold's (1907) holotype of *L. nuttalli* var. *antecedens,* a left valve, is USNM 165290.

*Material.* — The phenetic study was based on about 25 Recent and fossil specimens, all in the collections of the Yale Peabody Museum. Recent specimens were from southern California and Baja California. Pleistocene ones were from the upper San Pedro Formation, San Pedro, California; and from Pacific Grove, California (no stratigraphic data more specific than the age assignment were given on the specimen label). Forms to which a Pliocene age was attributed were from San Diego, California, (no specific stratigraphic data were given).

*Discussion.* — Keen (1958) stated that Recent representatives of this species are common on tide flats in southern California; the species ranges as far south as Tres Marias Islands, Mexico (near the southern tip of Baja California). It is a characteristic species of the upper Pleistocene shallow inner sublittoral association of Valentine (1961) in southern California. Grant and Gale (1931) cited numerous Pliocene and Pleistocene occurrences of *L. (Lucinisca) nuttalli,* and Nomland (1917) reported it from the upper Miocene Santa Margarita Formation, in southern California.

Dall (1901b) proposed the varietal name *centrifugus* for individuals with widely spaced concentric ribs, but Keen (1958) stated that "this character does not seem to be really significant even in the type area [the Gulf of California]". The "variety" *antecedens* named by Arnold (1907) whose type horizon is the Pliocene Fernando Formation, in Santa Barbara County, California, also differs from typical *L. nuttalli* only in having more widely spaced concentrics.

### Subgenus **PLEUROLUCINA**

*Dallucina* Olsson and Harbison, 1953, p. 87.
*Paslucina* Olsson, 1964, p. 47.

*Author.* — Dall, 1901b, p. 806.

*Type species.* — *Lucina leucocyma* Dall, 1886, pp. 264-265, by original designation.

*Discussion.* — Dall (1901b) proposed this subgenus as one of two sections of *Here,* which he considered a subgenus of *Phacoides.* As noted in the discussion of *Here,* Dall also included in that subgenus the species here placed in *Lucina* *s. s.* As mentioned earlier, Chavan (1937) assigned to *Pleurolucina* a number of species here included in *Bellucina.*

*Diagnosis.* — Shell of very small to small size, shape varying from slightly elongate to considerably higher than long, inflation moderate to very great, anterior expansion small to moderate. Surface sculpture of few (usually four) broad radial ribs, separated by deep furrows which produce an undulatory surface; boundaries between ribs tend to become indistinct, or disappear completely, ventrally and toward center of shell; concentric ribs fine; growth rings irregularly spaced, or present only on ventral part of shell. Dorsal areas conspicuous, anterior one forming pseudolunule. Lunule "figure-8" shaped, symmetrical, depth varying from shallow to excavated. Ligament external. Anterior adductor scar of normal length and width, generally curved, diverging from pallial line; posterior adductor scar elliptical. Anterior pedal retractor scar separate from adductor; posterior one partly separate in some species, not evident in others. Hinge plate wide; beaks moderately elevated; anterior and posterior cardinals single in right valve, double in left; one or two cardinals in right valve, two in left. Pallial blood vessel scar present.

*Distribution and phylogenetic relationships.* — *Pleurolucina* seems to be exclusively a Western Hemisphere subgenus. It is represented in the Recent fauna by *Lucina (Pleurolucina) leucocyma* Dall, 1886, a West Atlantic and Caribbean species, and by *L. (P.) undatoides* Hertlein and Strong, 1945, from the Gulf of California.

Olsson and Harbison (1953) proposed the name *Dallucina* (as a subgenus of *Phacoides*) for *Lucina amabilis* Dall, 1898, from the Pliocene Caloosahatchee Formation of Florida. As will be shown in the discussion of *L. (P.) amabilis,* this subgeneric name is unnecessary. *L. (P.) choctawhatcheensis* (Mansfield, 1916), from the late Miocene Choctawhatchee Formation of Florida, resembles the Recent *L. (P.) undatoides* and small specimens of *L. (P.) amabilis* in being moderately inflated and somewhat longer than high. *L. (P.) quadricostata* (Dall, 1903), from the middle Miocene Bowden Formation of Jamaica, more closely resembles adult *L. (P.) amabilis* and the Recent species *L. (P.) leucocyma,* being more strongly inflated and higher than long.

The earliest species to represent the *Pleurolucina* lineage is *Lucina (Paslucina) follis* Olsson, 1964, from an unnamed sandstone unit of probable early Miocene age in Ecuador. *Paslucina,* proposed by Olsson with *L. follis* as type, is here synonymized with *Pleurolucina. L. (P.) follis* closely resembles *L. (P.) leucocyma* in shape, size, dentition, dorsal areas, and musculature, but the four radial ribs are well marked on only the dorsal third of the shell. There are several deep growth rings clustered together near the ventral margin. The fading out ventrally of the radial sculpture is reminiscent of *Callucina;* many larger individuals of other species of *Pleurolucina* show a similar tendency.

A group of small species which have previously been assigned to *Here* seem to have their closest affinities with *Pleurolucina.* They have a deep but not excavated lunule; the dorsal areas are distinct or conspicuous; and the musculature is like that of *Pleurolucina.* In addition to the lines setting off the anterior and posterior dorsal areas, there is a radial sulcus on the anterior part of the shell, in approximately the same position as that defining the first radial rib of *Pleurolucina.* The shell thus has one narrow anterior rib and one broad central one. Species showing these features are *Lucina (Pleurolucina?) iduna* Olsson, 1932, from the early Miocene Montera Formation of Peru; *L. (P.?) tithonis* (Dall, 1903), from the middle Miocene Bowden Formation of Jamaica; and two Recent species, *L. (P.?) sombrerensis* Dall, 1886, and *L. (P.?) leucocymoides* (Lowe, 1935), from the Gulf of Mexico and the Gulf of California, respectively.

The shape of the lunule and the prominence of the dorsal areas in *Pleurolucina* recall *Lucina s. s.* and *Here.* In fact, the excavation of the lunule in *L. (P.) amabilis* and the shallower "figure-8" lunules of *L. (P.) leucocyma* and *L. (P.) undatoides* form a close parallel with the situation in *Here* and *Lucina s. s.* Forms such as *L. (P.?) iduna,* with only two radial ribs, may represent a transition between *Lucina s. s.* or *Here* and *Pleurolucina.* The dentition and musculature of *Pleurolucina* are most similar to those of *Cavilinga,* and the dorsoventrally elongated shape of several species of *Pleurolucina* recall the similarly elongated forms of *L. (C.) pomilia* and *L. (C.) trisulcata. Pleurolucina* thus may be a radially sculptured analogue of *Cavilinga.* Another possibility, suggested by Chavan's placement in *Bellucina* of some species here considered to belong to *Pleurolucina,* is that these two subgenera are closely related, both perhaps having been derived from *Parvilucina.*

### **Lucina (Pleurolucina) leucocyma** Dall

Plate 30, figures 1-4

*Lucina leucocyma* Dall, 1886, pp. 264-265; Dall, 1890a, p. 263, pl. 14, figs. 6-7.
*Phacoides (Pleurolucina) leucocyma* (Dall), Dall, 1901b, pp. 805, 808; Lamy, 1920, pp. 172, 205-206; Thiele, 1935, p. 866.
*Linga (Pleurolucina) leucocyma* (Dall), Chavan, 1937, pp. 211, 214.
*Lucina (Pleurolucina) leucocyma* Dall, Abbott, 1954, p. 387, figs. 78d, 78e.

*Description.* — Shell very small (median length of six specimens 5.4 mm, range 4.4-5.9 mm), higher than long (median H/L 1.16, range 1.11-1.19), very strongly inflated (median D/L 0.52, range 0.49-0.54), anterior expansion usually small (median A/L 0.44, range 0.37-0.58). Surface sculpture of four broad radial ribs, less distinctly separated toward center of shell and on its ventral portion; concentric ribs distinct, growth rings irregularly spaced. Dorsal areas and ligament as in generic diagnosis; lunule "figure-8"-shaped, shallow. Anterior adductor scar of normal length and width, curved away from pallial line; posterior one elliptical. Anterior pedal retractor scar separate and posterior one partly separate from adductors. Dentition as in generic diagnosis. Pallial blood vessel scar present; inner ventral margin denticulate.

*Types.* — The holotype of *Lucina leucocyma,* a bivalved specimen, is in the National Museum of Natural History (USNM 83140). The type locality is off Sombrero Island, in the Gulf of Mexico.

*Material.* — The phenetic study was based on six Recent specimens, all from Florida, in the collections of the Yale Peabody Museum, and on the holotype in the National Museum of Natural History.

*Discussion.* — Dall (1890a) gave the habitat of this species as "off the eastern coast of the United States, the Gulf of Mexico, and the West Indies". Abbott (1954) reported that it is found living "from low water to several fathoms". It is a distinctive species, and no problems of synonymy have arisen.

### **Lucina (Pleurolucina) undatoides** Hertlein and Strong

Plate 30, figures 5-8

*Lucina undata* Carpenter, 1865a, p. 279 [*non Lucina undata* Lamarck, 1818].
*Phacoides (Pleurolucina) undatus* (Carpenter), Dall, 1901b, pp. 811, 826, pl. 39, fig. 14; Lamy, 1920, p. 205.
*Linga (Pleurolucina) undata* (Carpenter), Chavan, 1937, pp. 212, 214, fig. 5.
*Lucina undatoides* Hertlein and Strong, 1945, p. 105.
*Lucina (Pleurolucina) undatoides* Hertlein and Strong. Keen, 1958, p. 96, fig. 195; Olsson, 1961, p. 209, pl. 31, fig. 13; Palmer, 1963, pp. 306-307, pl. 59, figs. 6-8.

*Description.* — Shell small (median length of 11 specimens 14 mm, range 10-16 mm), slightly longer than high (median H/L 0.94, range 0.82-0.95), moderately to strongly inflated (median D/L 0.30, range 0.25-0.34), anterior expansion moderate to great (median A/L 0.48, range 0.45-0.58). Surface sculpture as in *L. (P.) leucocyma.* Lunule as in *L. (P.) leucocyma,* but deeper; ligament and musculature as in *L. (P.) leucocyma.* Hinge plate narrower and beaks less elevated than in *L. (P.) leucocyma;* dentition as in *L. (P.) leucocyma,* except only one cardinal, not bifid, in right valve. Pallial blood vessel scar present; inner ventral margin denticulate; shell interior white or yellow.

*Types.* — As pointed out by Palmer (1963), because the name *L. undatoides* is a substitute name for Carpenter's *L. undata,* its type is the same as that of Carpenter's species. Hertlein and Strong had designated a specimen in the California Academy of Sciences as type of *L. undatoides.* Palmer figured as Carpenter's syntypes three valves in the collection of the Redpath Museum of McGill University (Redpath Mus. No. 122); they were collected in the Gulf of California.

*Material.* — The phenetic study was based on about 15 Recent specimens, all from La Paz, Baja California, in the collections of the Yale Peabody Museum.

*Discussion.* — This species apparently lives only in the Gulf of California (Keen, 1958). It is distinguished from *L. (P.) leucocyma* by its greater anterior-posterior elongation, lesser inflation, and larger size. In these respects it resembles small specimens of *L. (P.) amabilis* (compare Plate 30, figure 5, and Plate 30, figure 14). The depth of the lunule in this species is intermediate between that of *L. (P.) leucocyma* and that of *L. (P.) amabilis.*

### **Lucina (Pleurolucina) amabilis** Dall

Plate 30, figures 9-14

*Lucina (Here) amabilis* Dall, 1898, p. 920, pl. 25, figs. 9, 9a.
*Phacoides (Pleurolucina) amabilis* (Dall), Dall, 1903, pp. 1368-1369.
*Linga (Pleurolucina) amabilis* (Dall), Chavan, 1937, p. 214.
*Phacoides (Dallucina) amabilis* (Dall), Olsson and Harbison, 1953, pp. 87-88, pl. 7, fig. 2, 2a; DuBar, 1958, p. 169.

*Description.* — Shell very small (median length of 12 specimens 8.5 mm, range 5.7-10.9 mm), about 1.5 times higher than long (median H/L 1.48, range 1.37-1.61), very strongly inflated (median D/L 0.70, range 0.57-0.85), anterior expansion usually small (median A/L 0.42, range 0.36-0.50); smaller specimens are less strongly elongated dorsoventrally and less inflated. Surface sculpture as in *L. (P.) leucocyma,* with small specimens having radial ribs well marked over entire shell surface; radials of larger specimens become less distinct ventrally (cf. Plate 30, figure 14, and Plate 30, figure 10). Lunule "figure-8"-shaped, deeply excavated. Ligament external. Musculature as in *L. (P.) leucocyma,* except anterior adductor scar straight, diverging from pallial line, and posterior pedal retractor scar not evident. Dentition as in *L. (P.) leucocyma;* cardinals crowded together, but not effaced, by excavation of lunule. Pallial blood vessel scar present. Inner ventral margin smooth.

*Types.* — The specimens on which Dall based his description of *L. (P.) amabilis* are in the National Museum of Natural History. Two right valves, USNM 157806, labeled "types", are the specimens figured by Dall (1898). They are figures 9 to 11 in Plate 30 of this paper. About 20 additional specimens, also numbered USNM 157806, are labeled "syntypes". The specimens figured by Olsson and Harbison (1953) in their proposal of the subgenus *Dallucina* are in the Academy of Natural Sciences of Philadelphia (ANSP 18963).

*Material.* — The phenetic study was based on about 25 specimens, including Dall's types, in the National Museum of Natural History; all are from the Pliocene Caloosahatchee Formation of Florida.

*Discussion.* — Olsson and Harbison (1953) proposed a new subgenus *Dallucina* for this species. Though the deeply excavated lunule and the extreme dorsoventral compression of *L. (P.) amabilis* strikingly distinguish it from other species of *Pleurolucina,* it seems to fit well into the phylogenetic continuum outlined in the section on distribution and phylogenetic relationships of this subgenus. Both the earlier and the later relatives of *L. (P.) amabilis* have lunules which are shallow or moderately deep. As shown in the discussion of *L. (Lucina) pensylvanica* and *L. (Here) excavata,* the degree of excavation of the lunule may vary throughout ontogeny. I thus do not consider the name *Dallucina* necessary. The morphological differences between *Pleurolucina* and *Dallucina* are analogous to those between *Lucina s. s.* and *Here,* which are treated as distinct subgenera. *Here,* however, seems to have had a separate evolutionary history since Eocene time.

### ?Subgenus **RECURVELLA**

*Author.* — Chavan, 1937, p. 246.

*Type species.* — *Lucina dolabra* Conrad, 1833a, p. 343, by original designation.

*Discussion.* — Chavan (1937) proposed *Recurvella* as a subgenus of *Lucina (= Phacoides).*

*Diagnosis.* — Shell very small, higher than long, moderately to strongly inflated, anterior expansion moderate to great. Sculpture concentric, distinct, with growth rings irregularly spaced. Dorsal areas distinct or (particularly the posterior one) conspicuous; anterior one forms pseudolunule. No true lunule present; beaks strongly elevated and hooked forward. Ligament external. Anterior adductor scar rather short, but longer than that of *Parvilucina,* of normal width, straight or slightly curved, either parallel to or diverging from pallial line (Plate 30, figures 17 and 18); posterior adductor scar elliptical. Anterior pedal retractor scar separate and posterior one partly separate from adductors. Hinge plate wide, with one slightly bifid cardinal tooth in right valve, two cardinals in left; no lateral teeth. Pallial blood vessel scar present. Inner ventral margin denticulate.

*Distribution and phylogenetic relationships.* — The type species seems to be the only representative of this subgenus in North America. Chavan placed two European species, both from the French upper Eocene, in *Recurvella;* they are *Phacoides asymetricus* Cossmann, *in* Cossmann and Peyrot, 1911, and *Phacoides (Parvilucina) rozieri* Cossmann, 1921. The type species, from the middle Eocene of Alabama, is different from most other lucinids. The distinct dorsal areas indicate that it may be best placed as a subgenus of *Lucina.* It certainly is even less similar to *Codakia, Myrtea,* or *Anodontia.* The prominence of the cardinals and absence of laterals may indicate a relationship to *Miltha,* but species of *Miltha* are characteristically much larger than is *R. dolabra. Recurvella* may be an early offshoot of the *Lucina s. s.* or *Callucina-Parvilucina* lineage; it apparently became extinct relatively soon after its origin and gave rise to no other groups. The type species is abundant at the type locality, the Gosport Sand of Claiborne, Alabama; but Chavan (1937) stated that both of the late Eocene species which he referred to this subgenus are rare.

### **Lucina? (Recurvella) dolabra** Conrad

Plate 30, figures 15-19

*Lucina dolabra* Conrad, 1833a, p. 343; Conrad, 1833c, p. 40; Harris, 1919, p. 111, pl. 37, figs. 17-21; E. J. Moore, 1962, p. 55.
*Lucina (Recurvella) dolabra* Conrad, Chavan, 1937, pp. 246-247, fig. 7; Palmer and Brann, 1965, pp. 181-182.
*Astarte recurva* Lea, 1833, p. 61, pl. 2, fig. 34.

*Description.* — Shell very small (median length of 14 specimens 7.6 mm, range 5.1-10.1 mm), higher than long (median H/L 1.04, range 1.00-1.12), moderately to strongly inflated (median D/L 0.35, range 0.26-0.40), anterior expansion moderate to great (median A/L 0.48, range 0.37-0.56). Other characters as in generic diagnosis.

*Types.* — E. J. Moore (1962) listed eight valves of this species in the Academy of Natural Sciences of Philadelphia (ANSP 30523) as Conrad's "probable syntypes". I was unable to find specimens of *Astarte recurva* Lea at the Philadelphia Academy. The specimens figured by Harris (1919) are in the Paleontological Research Institution (PRI 726-731).

*Material.* — The phenetic study was based on about 50 specimens, all from the Gosport Sand, in the collections of the National Museum of Natural History. Conrad's specimens at the Academy of Natural Sciences of Philadelphia, and Harris's specimens at the Paleontological Research Institution were subsequently examined.

*Discussion.* — The extremely elevated and recurved beaks are the most characteristic feature of this species. A dorsal view (Plate 30, figure 19) shows the conspicuous anterior dorsal area, resembling in shape and in relative size that of *L. (Lucina) pensylvanica.* Authors who have previously discussed this species have referred to this area as a lunule, but it seems to be clearly homologous with the anterior dorsal area of other lucinids. *Recurvella dolabra* thus has no structure which is homologous with the lunule of other lucinids.

Carter (1967a, 1967b) discussed the definition and morphological significance of the lunule in the Bivalvia. He believed that the form of the lunule has no true functional significance but is simply a necessary geometric consequence of the relative positions of the plane of commissure of the shell and of the directive plane (that plane in which the axis of coiling of the shell is a logarithmic spiral). It is difficult to accept his concept completely for the lucinids, because in his discussion of this group he has not distinguished between the lunule and the anterior dorsal area (Carter, 1967a, pl. 35, figs. I and K). It does, however, seem reasonable to agree with his conclusion that the lunule fills in the gap in front of the beaks which arises as a consequence of the coiling of the shell in the umbonal region. In *Lucina? (Recurvella) dolabra,* the elevation of the beaks is accentuated by the failure of the lunule to develop.

### Genus **CODAKIA**

### Subgenus **CODAKIA**

*Lentillaria* Schumacher, 1817, p. 49, 147.
*Antilla* de Gregorio, 1885, p. 214.
*Codokia* Recluz, 1869, p. 35.
*Pexocodakia* Iredale, 1930b, p. 389.

*Author.* — Scopoli, 1777, p. 398.

*Type species.* — *Chama, le codok* Adanson, 1757, p. 223, pl. 17, fig. 3 (non-binomial) (?= *Venus orbicularis* Linné, 1758, p. 688, or ? = *Venus tigerina* Linné, 1758, p. 688), by monotypy.

*Discussion.* — Scopoli (1777) proposed the name *Codakia* for a shell described by Adanson (1757) under the name *"le codok"*, one of several species which Adanson included in *"Chama"*. Having been proposed a year before the publication of the tenth edition of *Systema Naturae,* Adanson's name has no status in nomenclature. His species has been identified with both of two Linnean species, *Venus orbicularis* and *V. tigerina* [see discussion of *Codakia (Codakia) orbicularis*]. Fischer (1887) apparently considered *V. tigerina* and *"le codok"* synonymous. Dall (1903) stated that "it is uncertain whether [*"le codok"*] is identical with [*V. tigerina*] or [*V. orbicularis*], though the probabilities are in favor of the latter". Lamy (1920) and Chavan (1937) accepted *V. orbicularis* as type of *Codakia. V. orbicularis* is a West Indian shell, and Fischer-Piette (1942) pointed out that although Adanson described it as a Senegalese shell, before the preparation of the description Adanson's Senegalese specimens may have been mixed with shells brought to him by travelers from other regions. It is also possible that *V. tigerina,* which most workers have interpreted as being from the Indo-Pacific, is actually conspecific with *V. orbicularis* (Dodge, 1952).

Scopoli, misspelling Adanson's name *"codok"* as *"codak"*, made the generic name accordingly. Recluz (1869) and Fischer (1887) thus emended *Codakia to Codokia.* Dall (1901b, 1903) did not accept this emendation, but Lamy (1920), Chavan (1937), and Dodge (1952) have done so. According to the International Code of Zoological Nomenclature [Art. 32a()(ii)], the name of a taxon may be emended if "there is in the original publication clear evidence of an inadvertent error, such as a lapsus calami, or a copyist's or printer's error". It is apparent that Scopoli intended the generic name *Codakia* to be based on the name of Adanson's species, but there is no "clear evidence" indicating whether or not the change in spelling was deliberate. Because Adanson's name is pre-Linnean, it does not seem necessary to emend *Codakia* to bring it into consonance with a name which is not available. *Codakia* was in use for a hundred years prior to Fischer's emendation and still seems to be more widely used than *Codokia.* In his contribution to the *Treatise on Invertebrate Paleontology,* Chavan (1969) used *Codakia.* For these reasons I also prefer to employ the original spelling of the name.

The genera here synonymized with *Codakia* and their type species are as follows: *Lentillaria* Schumacher, 1817 (*Venus punctata* Linné, 1758); *Antilla* de Gregorio, 1885 (*Venus tigerina* Linné) — an objective synonym of *Codakia* if *V. tigerina* is synonymous with *le codok* or with *V. orbicularis;* and *Pexocodakia* Iredale, 1930b (*L. rugifera* Reeve, 1850). *V. punctata* and *L. rugifera* are distinguished from *C. orbicularis* by variations in the coarseness of the surface sculpture and in the relative strengths of concentric and radial sculpture.

Chavan (1937) did not consider *Codakia* to have been properly proposed because of the brevity and imprecision of the generic diagnosis and the lack of an exact reference to Adanson's species; in the 1937 paper he used *"Codakia"* as a general term for a taxon which he divided into two subgenera, *Epilucina* and *Lentillaria.* His subsequent treatment of the lucinids (Chavan, 1969), however, followed the requirements of the International Code by using *Codakia* rather than *Lentillaria* for the nominate subgenus.

*Diagnosis.* — Shell of medium to very large size, longer than high, flat to moderately inflated, anterior expansion small. Surface sculpture predominantly radial, with ribs generally numerous and fine, in some species becoming broader and flatter at center of disk; radials occasionally bifurcating; concentrics numerous, threadlike; growth rings irregularly spaced. Dorsal areas faint. Lunule triangular, narrow, deep, short, strongly asymmetrical, with projection in right valve fitting into recess in left. Ligament short, broad, triangular, deeply inset (Pl. 31, fig. 2). Anterior adductor scar of normal length and width, curved away from pallial line; posterior adductor scar elliptical; neither pedal retractor scar evident. Hinge plate wide; anterior laterals single in right valve, double in left; posterior laterals virtually or completely effaced by broad, inset ligament. Two cardinals in each valve; right anterior cardinal strong, but sometimes partly effaced by deep lunule; right posterior cardinal not bifid. Shell interior, especially hinge plate and portion outside pallial line, often colored. Pallial blood vessel scar present; inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — *Codakia s. s.* is one of the most widely distributed of Recent lucinid subgenera. Lamy (1920) lists eight Recent species, of which three are North American and the others Indo-Pacific. The Recent *Codakia (Codakia) orbicularis* (Linné), from the southeastern United States, the Caribbean, and possibly also Senegal, has persisted unchanged since at least Pliocene time (Dall, 1903). Maury (1917) also reported it from the Miocene of the Dominican Republic. Its West Coast analogue, *C. (C.) distinguenda* Tryon, 1872, whose present range is from the Gulf of California to Panama, is reported from the Pliocene of Baja California (Durham, 1950) and the Pleistocene of southern California and Baja California (Grant and Gale, 1931).

Two middle Miocene species of *Codakia s. s.*, both from the Bowden Formation of Jamaica, have been described; they are *Codakia spinulosa* Dall, 1903, and *C. lomonea* Woodring, 1925. *C. spinulosa* differs from *C. orbicularis* only in having finer radial sculpture and in being smaller. It resembles the Recent *Codakia cubana* Dall, 1901b, from the Cuban coast. The sculpture of *C. lomonea* is similar to that of *C. orbicularis,* but the shell is considerably smaller (length of the holotype 14 mm) and more anteriorly expanded, and the ligament, though deeply inset, does not efface the posterior laterals. This species may represent a transition between *Codakia (Codakia)* and *Codakia (Ctena).*

Chavan (1937) stated that *Codakia s. s.* is principally a Miocene to Recent subgenus, though he listed one species, *C. (Codakia) gravesi* (Deshayes) from the Paleocene of the Paris Basin. I have not seen this species, which Chavan stated is rare and poorly preserved. European Eocene species which previous workers had assigned to *Codakia* were placed by Chavan in *Epilucina* or *Callucina.* Even though the subgenus may be of early Tertiary origin, at any rate it was not abundant or diverse until about middle Miocene time.

### **Codakia (Codakia) orbicularis** (Linné)

Plate 31, figures 1-5

*Venus orbicularis* Linné, 1758, p. 688.
*Codakia orbicularis* (Linné), Dall, 1901b, p. 799; Dall, 1903, p. 1347; ? Maury, 1917, p. 366, pl. 35, fig. 1.
*Codokia (Codokia) orbicularis* (Linné), Lamy, 1920, pp. 235-237; Thiele, 1935, p. 868.
*Codokia (Lentillaria) orbicularis* (Linné), Chavan, 1937, pp. 271, 279, 280-281; Weisbord, 1964, pp. 226-229, pl. 30, figs. 1-8.
*Codakia (Codakia) orbicularis* (Linné), Abbott, 1954, p. 390, pl. 38d; Warmke and Abbott, 1961, p. 178, pl. 36g.
*Codakia (Ctena) orbicularis* (Linné), DuBar, 1958, p. 166.
*Venus tigerina* var. β Linné, 1767, p. 1134.
? *Codakia codak* Scopoli, 1777, p. 398.
? *Venus tigerina* Linné, 1758, p. 688; Linné, 1767, p. 1133 [No. 136].
? *Venus tigerina* Linné, 1767, p. 1134 [No. 141].
? *Antilla tigerina* (Linné), de Gregorio, 1885, pp. 214-215.
? *Codakia tigerina* (Linné), Dall, 1901b, p. 798, 801.
? *Codokia tigerina* (Linné), Fischer, 1887, p. 1143; Lamy, 1920, pp. 239-241.
? *Codokia (Lentillaria) tigerina* (Linné), Chavan, 1937, pp. 280-281.

*Description.* — Shell large (median length of 23 specimens 46 mm, range 8-65 mm), longer than high (median H/L 0.89, range 0.83-0.95), flat to moderately inflated (median D/L 0.21, range 0.14-0.24), anterior expansion small except in juveniles (median A/L 0.43, range 0.38-0.55). Sculpture coarse, dominantly radial, radials rarely bifurcating; concentric ribs less prominent, thin; growth rings irregularly spaced; dorsal areas faint, marked only by radial sculpture being slightly more closely spaced than on rest of disk. Lunule, ligament, musculature, and dentition as in generic diagnosis. Shell interior yellow, or with hinge plate and band outside pallial line pink and portion of shell within pallial line white or yellow. Pallial blood vessel scar present; inner ventral margin smooth.

*Types.* — Fischer-Piette (1942, p. 306) illustrated Adanson's molluscan collection, now housed in the Muséum nat. d'Hist. nat. in Paris. "*Chama, le codok*" is figured on plate 14, figure 3. A specimen identified by Linné as *Venus orbicularis* is in the collection of the Linnean Society of London. Linné numbered consecutively the species in each major taxon of his *Systema Naturae,* and, confusingly, this specimen bears the number given to *V. orbicularis* in the tenth edition of this work as well as that given to the first description of *V. tigerina* in the twelfth edition (see discussion below). No unambiguously identified specimen of *V. tigerina* is in the Linnean collection (Dodge, 1952).

*Material.* — The phenetic study was based on about 30 specimens, mostly Recent ones from Florida, the Bahamas, Jamaica, Tobago, and the Barbados, but including a few Pleistocene ones from Florida and Venezuela. All are in the collections of the Yale Peabody Museum.

*Discussion.* — Dodge (1952) summarized the problems of nomenclature of the species *Venus orbicularis* Linné and *V. tigerina* Linné. In the tenth edition of *Systema Naturae,* Linné (1758) straightforwardly treated *tigerina* and *orbicularis* as distinct species. The habitat of the first was given as the Indian Ocean; that of the second, only as "intra tropicos". In the twelfth edition, Linné used the name *Venus tigerina* on two successive pages (Linné, 1767, pp. 1133, 1134), with slightly different descriptions. In the first description (No. 136 in Linné's species list), the habitat of *V. tigerina* was given as the Indian Ocean; in the second (No. 141), it is given as "intra tropicos". *V. orbicularis* was treated as a variety of *V. tigerina* in the second description. Dodge considered the description of *V. tigerina* No. 136 of the twelfth edition to correspond to that of *V. tigerina* in the tenth edition, but he found the problem of the second *V. tigerina* (No. 141 of the twelfth edition) to be insoluble. As he pointed out, the major difference between the descriptions 136 and 141 is that the latter includes a reference to the pink shell interior which is characteristic of *V. orbicularis.* My inference is that Linné's intention in the twelfth edition was to synonymize *orbicularis* with *tigerina,* coalescing the descriptions of the two species and giving the more inclusive habitat attributed to *orbicularis* in the tenth edition; but that he mistakenly left in the earlier description of *tigerina* alone. The fact that the same specimen seems to be identified with both *orbicularis* and *tigerina* (see discussion of types above) may lend credence to this interpretation. If *orbicularis* and *tigerina* are indeed conspecific, this would be the only lucinid species known to have such a wide range.

Abbott (1954) gave the North American distribution of *C. orbicularis* as "Florida to Texas and the West Indies". It also occurs in Bermuda (Dall, 1901b). It is largely restricted to grass-covered sandy bottoms and lives in the low intertidal-shallow subtidal environment, preferring somewhat less stressful conditions than those which the co-occurring *Lucina (Phacoides) pectinata* tolerates in tidal flat areas (Stanley, 1970). As pointed out long ago by Dall (1903), small individuals of *C. (C.) orbicularis* tend to be more strongly expanded anteriorly than larger ones (cf. pl. 7, figs. 1, 4). Externally they thus closely resemble *C. (Ctena) orbiculata,* but the characteristic inset ligament, effacing the posterior laterals, is present on small as well as large specimens of *C. (C.) orbicularis.* Individuals of the two species of about the same size can also be distinguished by the much greater incidence of bifurcation of the radial ribs in *C. (Ctena) orbiculata.*

### **Codakia (Codakia) distinguenda** (Tryon)

Plate 31, figures 6, 7

*Lucina (Codakia) tigerina* Carpenter, 1857, pp. 96-97 [*non Venus tigerina* Linné, 1758].
*Lucina (Codakia) distinguenda* Tryon, 1872, p. 130, pl. 6, fig. 3.
*Codakia distinguenda* (Tryon), Dall, 1903, p. 1345; Grant and Gale, 1931, p. 283; Keen, 1958, p. 98, fig. 200.
*Codokia distinguenda* (Tryon), Lamy, 1920, pp. 238-239.
*Codokia (Lentillaria) distinguenda* (Tryon), Chavan, 1937, p. 281.
*Codakia (Codakia) distinguenda* (Tryon), Olsson, 1961, p. 217, pl. 29, fig. 3; pl. 33, figs. 4, 4a.
*Codakia colpoica* Dall, 1901b, p. 801, 821, pl. 41, fig. 4.

*Description.* — Shell thick, very large (median length of 24 specimens 67 mm, range 32-118 mm), longer than high (median H/L 0.89, range 0.85-0.95), flat to moderately inflated (median D/L 0.20, range 0.14-0.24), anterior expansion small (median A/L 0.40, range 0.33-0.49). Surface sculpture as in *C. (C.) orbicularis* bus less coarse. Lunule of smaller individuals identical to that of *C. (C.) orbicularis;* in larger individuals nearly oval in shape. Ligament, dentition, musculature, and other internal features as in *C. (C.) orbicularis,* except that pink rim outside pallial line is more consistently present and deeper in color.

*Types.* — According to Grant and Gale (1931), the holotype of this species is in the Academy of Natural Sciences of Philadelphia.

*Material.* — The phenetic study was based on about 25 Recent specimens, from the Gulf of California and Panama; all are in the collections of the Yale Peabody Museum.

*Discussion.* — Grant and Gale (1931) believed that *C. distinguenda* might be conspecific with *C. orbicularis.* The principal differences between the two are the larger size and stronger coloration of the West Coast species. The difference in shape of the lunule, one of the major criteria by which Dall (1901b) separated the East Coast and West Coast species, is seen only in individuals of *C. distinguenda* which have attained a larger size than that reached by adults of *C. orbicularis.* Representatives of the two species of about equal size both have triangular lunules. If not conspecific, the two species are doubtless of common origin, having evolved separately only since the elevation of the Panamanian region in Pliocene time. Like many other West Coast bivalves, *C. distinguenda* ranged farther north in Pleistocene time than it now does (Grant and Gale, 1931). Dall (1901b) proposed the name *C. colpoica* for the West Coast species, but later he became aware of Tryon's prior name for it (Dall, 1903).

### Subgenus **CTENA**

*Jagonia* Récluz, 1869, p. 37.

*Author.* — Mörch, 1861, p. 201.

*Type species.* — *Codakia (Jagonia) mexicana* Dall, 1901b [= *Lucina pectinata* Carpenter, 1857, *non Lucina pectinata* C. B. Adams, 1852], by subsequent designation (Dall, Bartsch, and Rehder, 1938, p. 128).

*Discussion.* — Mörch (1861) introduced the name *Ctena* as a subgenus of *Codakia.* He included two species, *Codakia (Ctena) pectinata* (Carpenter) and *Codakia (Ctena) cancellaris* (Philippi). The second species is now assigned to *Bellucina.* Dall (1901b, 1903) originally rejected *Ctena* as a homonym of *Ctenia* Lepelletier and Serville (Insecta). Later, recognizing that generic names differing by a single letter are not homonyms, Dall, Bartsch, and Rehder (1938) reinstituted the use of *Ctena.* They designated *Codakia (Jagonia) mexicana* Dall, a replacement name for *Lucina pectinata* Carpenter, as type of *Ctena.*

Dall (1901b) substituted the name *Jagonia* Récluz, 1869, for *Ctena.* Récluz meticulously described his genus, giving an account of the soft-part anatomy as well as of the shell, and discussing several species which were to be included in the genus. The name *Jagonia* was taken from Adanson's *"le jagon"*, a presumably Senegalese species which Adanson had placed in *"Pectunculus"*, and which Récluz chose as the type of *Jagonia.* Chavan (1937) believed that *Jagonia* should be used instead of *Ctena* which was introduced without any description or diagnosis. The International Code of Zoological Nomenclature provides, however, that any new genus-group name is available if one or more available specific names have been cited in combination with it. Chavan (1946a) later designated *Lucina cancellaris* Philippi, 1846, as the type of *Ctena,* in order to preserve the name *Jagonia* by making *Ctena* synonymous with *Bellucina.* He was unaware, however, of the previous designation by Dall, Bartsch, and Rehder.

*Diagnosis.* — Shell of small to medium size, longer than high, moderately inflated, anterior expansion generally more than half of total length. Surface sculpture of radial and concentric ribs; radials dominant, usually 20 or more, frequently bifurcating; growth rings usually irregularly spaced. Dorsal areas faint to distinct, both set off only by increase in density of radial ribs. Lunule long, narrow, oval, shallow, symmetrical. Ligament external (like that of *Lucina* rather than that of *Codakia s. s.*). Anterior adductor scar of normal length and width, curved away from pallial line; posterior adductor scar elliptical. Anterior pedal retractor scar separate from adductor; posterior one not evident. Hinge plate narrow; anterior and posterior laterals single in right valve, double in left; two cardinals in each valve, but right anterior cardinal may be somewhat reduced; right posterior cardinal slightly bifid. Pallial blood vessel scar present; inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — The present distribution of *Ctena* is worldwide, at least in warm waters. Species of *Ctena* occur in West Africa, the Mediterranean, the southeastern United States and the Caribbean, Bermuda, the region from the Gulf of California to Panama, northwestern South America, the Indian Ocean, Australia, the Philippines, and Hawaii (Dall, 1901b; Lamy, 1920). Lamy (1920) summarized the complex problems of synonymy in the Recent species of *Ctena;* there may be anywhere from five to fifteen living species of the subgenus.

The type species of *Ctena, Codakia (Ctena) mexicana* Dall, is found living from the Gulf of California to Ecuador (Keen, 1958). Keen also listed four other species which occur less commonly in this area: *C. (C.) chiquita* Dall, 1901b; *C. (C.) clarionensis* (Hertlein and Strong, 1946); *C. (C.) clippertonensis* (Bartsch and Rehder, 1939); and *C. (C.) galapagana* Dall, 1901b. Possibly some of these forms are conspecific: *chiquita, galapagana,* and *mexicana* are all similar except for differences in size and in strength of the surface sculpture. *C. (C.) mexicana* is found as an upper Pliocene and Pleistocene fossil in eastern Baja California (Durham, 1950); Durham also reported *C. (C.) chiquita* from the Pleistocene of the same area. The Recent West Atlantic and Caribbean analogue of *C. (C.) mexicana, C. (C.) orbiculata* (Montagu, 1808), is also reported from strata of Pliocene and Pleistocene age (Dall, 1903; Olsson and Harbison, 1953). It may be identical with the West African species *Venus eburnea* Gmelin, 1791 (= *"Pectunculus, le jagon"* Adanson, 1757). Dall (1901b) recognized four "varieties" of *C. (C.) orbiculata;* the distinctions between these are analogous to those which define the West American species of *Ctena.*

Though some of the species previously placed in *Ctena* are here referred to *Parvilucina* or *Callucina, Ctena* remains one of the most abundantly represented lucinid groups in the fossil record. Several species from the late Miocene of North America — *Codakia (Ctena) speciosa* (Rogers and Rogers, 1837), from the Yorktown Formation of Virginia and the Duplin Marl of North Carolina; *C. (C.) magnoliana* Dall, 1903, from the Duplin Marl and the Choctawhatchee Formation of Florida; and *C. (C.) microimbricata* (Gardner, 1944), from the Duplin Marl — have been distinguished primarily on differences in the relative coarseness of the surface sculpture.

An interesting late Miocene species which probably belongs to *Ctena* is *Codakia (Ctena?) leonensis* Mansfield, 1937, from the Choctawhatchee Formation (late Miocene, Florida). The strong anterior expansion of the shell recalls *Ctena,* but the radial sculpture consists of only about six large radial ribs, with one to three smaller radials intercalated on the ventral half of the shell. The surface sculpture is reminiscent of that of *Bellucina,* except that the dorsal areas are only faintly indicated. Unfortunately, the musculature of Mansfield's specimens (USNM 371179) is poorly preserved. Perhaps this species represents a branch of the *Ctena* lineage in which reduction in number and increase in size of the radials occurred, paralleling the similar trend in the *Lucina* lineage which produced *Bellucina.* No other species similar to *leonensis* are known to me.

A middle Miocene species which is closely similar to Recent species of *Ctena* is *Codakia (Ctena) magnolioides* Maury, 1910, from the Alum Bluff Group of Florida. Another middle Miocene species, from the Bowden Marl of Jamaica, is *C. (C.) pertenera* Dall, 1903, which Dall stated "is not a typical [*Ctena*], but is nearer to this group than to any other." It resembles other species of *Ctena* in its marked anterior expansion, lunule shape, musculature, and ligament. Radial sculpture is fairly distinct on small specimens but present only on the umbonal region of larger ones (Woodring, 1925). Lateral teeth are completely lacking, and there is only one cardinal in the right valve. The size of the species (length of the holotype, USNM 135716, is 36 mm), is somewhat greater than that of other species of *Ctena.* Woodring (1925) placed *pertenera* in *Myrtea;* the absence of laterals and limitation of the surface sculpture to the umbonal region are reminiscent of *Callucina.* The shape of the shell and the musculature indicate, however, that Dall's original assignment to *Ctena* was correct.

Another Bowden species, *Codakia (Codakia) lomonea* Woodring, 1925, was discussed under *Codakia* as a possible morphological intermediate between *Codakia s. s.* and *Ctena* (see also below).

No internal features of the early Miocene *C. (Ctena) scurra* Dall, 1915, from the Tampa Limestone of Florida, are known; but the size, shape, and sculpture of this species indicate affinity with *Ctena.*

I have seen no North American Eocene or Oligocene species which may be referred to *Ctena,* but Chavan (1937) reported that the subgenus can be traced continuously from late Eocene through Miocene time in Europe. An Upper Cretaceous (Maestrichtian) species from the Navarro Group of Texas, *Lucina parvilineata* Shumard, 1860, may be the earliest known representative of *Ctena.* No internal features of the species are preserved on the National Museum of Natural History specimens collected by Stephenson (1941), but the small size, strong anterior expansion, presence of faint radials, and virtual absence of dorsal areas indicate affinity with *Ctena.* The lunule is shorter, wider, and deeper than in most species of *Ctena;* in this respect the species resembles *Codakia.*

Mörch (1861) proposed *Ctena* as a subgenus of *Codakia;* Dall (1901b), though using the junior synonym *Jagonia,* followed Mörch's taxonomic precedent. Chavan (1937) treated *Codakia* and *Ctena* as separate genera, believing that the differences in dentition, shell shape, and lunule shape entitled *Ctena* to generic status; he also stated that he knew of no common ancestor of the two taxa. In his more recent classification (Chavan, 1969), he continued to place them as different but related genera. Nevertheless, the differences in lunule shape are no greater than those between the lunules of some subgenera of *Lucina,* or even species of the subgenus *Lucinisca.* As previously stated, juveniles of *Codakia orbicularis* are as strongly expanded anteriorly as are adults of species of *Ctena.* Variations in the degree to which the ligament is inset can be seen in different subgenera of *Miltha* — in fact, in different individuals of the species *M. (Lucinoma) filosa* — and the loss of the posterior laterals in *Codakia* seems clearly to be a consequence of the internalization and broadening of the internal ligament. For these reasons it seems valid to treat *Codakia s. s.* and *Ctena* as only subgenerically different.

Though no single species can be unequivocally pointed out as a link between *Codakia* and *Ctena,* the middle Miocene *C. (Codakia) lomonea* is morphologically though apparently not stratigraphically intermediate between the two taxa. It may well, however, be ancestral to the several North American Pliocene to Recent species of *Codakia.* Though the status of the small Late Cretaceous *Codakia? (Ctena?) parvilineata* (Shumard, 1860) remains ambiguous without knowledge of its dentition and musculature, it has some morphological features (shell shape) which indicate relationship to *Ctena,* and others (shape and depth of lunule) which are similar to those of *Codakia.*

A Recent Australian species, *Epicodakia gunnamatta* Iredale, 1930b, is also morphologically intermediate between *Codakia* and *Ctena.* It has a deeply inset, triangular ligament [which Chavan (1938) stated becomes more nearly internal on larger specimens], but both anterior and posterior laterals are present, and the radial ribs are bifurcate. Chavan (1938) considered *Epicodakia* a subgenus of *Codakia,* but latter (Chavan, 1969) gave it separate generic status. I consider *Codakia s. s.*, *Ctena*, *Epicodakia*, and *Claibornites* (discussed below) all to be subgenera of *Codakia*.

### **Codakia (Ctena) mexicana** Dall

Plate 32, figures 1-4

*Lucina pectinata* Carpenter, 1857, pp. 98-99 [*non Lucina pectinata* C. B. Adams, 1852].
*Codakia (Ctena) pectinata* (Carpenter), Mörch, 1861, p. 201.
*Codakia (Jagonia) mexicana* Dall, 1901b, pp. 801, pl. 40, fig. 6; Durham, 1950, pp. 74-75, pl. 18, figs. 7, 14.
*Codokia (Jagonia) mexicana* Dall, Lamy, 1920, p. 252-253.
*Jagonia (Jagonia) mexicana* (Dall), Chavan, 1937, pp. 256, 260; Chavan, 1946a, p. 87.
*Ctena mexicana* (Dall), Dall, Bartsch, and Rehder, 1938, p. 128; Keen, 1958, p. 100, fig. 205.
*Codakia (Ctena) mexicana* Dall, Olsson, 1961, p. 218, pl. 29, fig. 5.
? *Codakia (Jagonia) galapagana* Dall, 1901b, pp. 801, 823, pl. 40, fig. 4.
? *Codokia (Jagonia) galapagana* (Dall), Lamy, 1920, p. 254.
? *Jagonia (Jagonia) galapagana* (Dall), Chavan, 1937, p. 260.
? *Ctena galapagana* (Dall), Keen, 1958, p. 100, fig. 204.
? *Codakia (Ctena) galapagana* Dall, Olsson, 1961, p. 218, pl. 29, fig. 5.
? *Codakia (Jagonia) chiquita* Dall, 1901b, pp. 801, 822, pl. 39, fig. 1; Durham, 1950, p. 74, pl. 18, figs. 6, 18.
? *Codokia (Jagonia) chiquita* (Dall), Lamy, 1920, p. 254.
? *Jagonia (Jagonia) chiquita* (Dall), Chavan, 1937, p. 260.
? *Ctena chiquita* (Dall), Keen, 1958, p. 100, fig. 201.

*Description.* — Shell of small to medium size (median length of 10 specimens 16 mm, range 6.5-23 mm), longer than high (median H/L 0.92, range 0.88-1.02), moderately inflated (median D/L 0.26, range 0.22-0.28), anterior expansion moderate to great (median A/L 0.52, range 0.43-0.59). Surface sculpture of radial and concentric ribs, radial sculpture predominating; nearly every radial rib bifurcates once, near umbo; concentric ribs slightly finer than radials; growth rings irregularly spaced. Dorsal areas faint, set off only by slight decrease in size of, and by crowding together of, radial ribs. Lunule long, narrow, oval, symmetrical, shallow. Ligament external. Anterior adductor scar of normal length and width, curved away from pallial line; posterior valve, double in left. Two cardinals in each valve; right adductor scar elliptical. Anterior pedal retractor scar separate from adductor, posterior one not evident. Hinge plate narrow; anterior and posterior cardinals single in right posterior cardinal slightly bifid. Shell interior white or light yellow. Pallial blood vessel scar present; inner ventral margin of shell not denticulate, but fluted by terminations of radial ribs.

*Types.* — Carpenter's original specimens of *Lucina pectinata* are in the Mazatlán mollusk collection at the British Museum (Natural History) (Keen, 1968, p. 396, pl. 56, fig. 21 holotype). The original of Dall's figure of *Codakia (Jagonia) mexicana* is in the National Museum of Natural History (USNM 101783), as are the types of his *C. (J.) galapagana* (USNM 102454) and *C. (J.) chiquita* (USNM 96563), tentatively synonymized above with *mexicana*.

*Material.* — The phenetic study was based on about 15 Recent specimens, all from La Paz, Baja California, except for one specimen labeled only "California". All are in the collections of the Yale Peabody Museum. The type and figured specimens mentioned above were subsequently examined.

*Discussion.* — Dall (1901b) proposed the name *Codakia (Jagonia) mexicana* as a replacement for *Lucina pectinata* Carpenter, 1857 [not *Tellina pectinata* Gmelin, 1791, the type species of *Phacoides;* nor *Lucina pectinata* C. B. Adams, 1852, which Dall (1901b) considered synonymous with the Caribbean *Codakia (Ctena) orbiculata*]. Dall (1901b) also named two other Eastern Pacific species of *Ctena: Codakia (Jagonia) galapagana,* from the Galapagos Islands, and *C. (Jagonia) chiquita,* from Baja California. They were distinguished from *C. mexicana* by having, respectively, coarser and finer radial sculpture; *C. chiquita* is also smaller and has weaker laterals than *C. mexicana. C. galapagana* is common intertidally in the Galapagos Islands (Dall, 1901b; Keen, 1958). *C. chiquita,* however, is rare (Keen, 1958), it may be only the juvenile of *mexicana.*

### **Codakia (Ctena) orbiculata** (Montagu)

Plate 32, figures 5-7

*Venus orbiculata* Montagu, 1808, p. 42, pl. 29, fig. 7.
*Codakia (Jagonia) orbiculata* (Montagu), Dall, 1901b, pp. 798, 799; Dall and Simpson, 1901, p. 491; Dall, 1903, pp. 1350-1351; Weisbord, 1964, pp. 229-232, pl. 31, figs. 1-4.
*Codakia (Jagonia) orbiculata* var. *orbiculata* (Montagu), Dall, 1901b, p. 799-800.
*Jagonia (Jagonia) orbiculata* (Montagu), Chavan, 1937, pp. 257, 260.
*Codakia (Ctena) orbiculata* (Montagu), Abbott, 1954, p. 391, pl. 30L; Warmke and Abbott, 1961, p. 178, pl. 36h.
*Codakia (Ctena) orbiculata* subsp. Olsson and Harbison, 1953, p. 79.
*Lucina pecten* Lamarck, 1818, p. 543 [*fide* Dall, 1901b].
? *Venus eburnea* Gmelin, 1791, p. 3292.
? *Jagonia jagon* Récluz, 1869, pp. 37, 39.
*Codokia (Jagonia) jagon* (Récluz), Lamy, 1920, pp. 246-248 [part].
? *Lucina imbricatula* C. B. Adams, 1845, p. 10.
? *Codakia (Jagonia) orbiculata* var. *imbricatula* (C. B. Adams), Dall, 1901b, p. 800.
? *Codokia (Jagonia) imbricatula* (C. B. Adams), Lamy, 1920, pp. 249-250.
? *Jagonia (Jagonia) imbricatula* (C. B. Adams), Chavan, 1937, p. 260.
? *Codakia (Jagonia) imbricatula* (C. B. Adams), Weisbord, 1964, p. 232, pl. 31, figs. 5, 6.
? *Lucina pectinata* C. B. Adams, 1852, p. 245.
? *Codakia (Jagonia) orbiculata* var. *filiata* Dall, 1901b, p. 800.
? *Codakia (Jagonia) imbricatula* var. *filiata* Dall, Lamy, 1920, p. 250.
? *Codakia (Jagonia) orbiculata* var. *recurvata* Dall, 1901b, p. 800.
? *Codakia (Jagonia) imbricatula* var. *recurvata* Dall, Lamy, 1920, p. 250.

*Description.* — Shell of small size (median length of 24 specimens 12 mm, range 7-20 mm), longer than high (median H/L 0.92, range 0.85-0.96), moderately to strongly inflated (median D/L 0.27, range 0.21-0.36), anterior expansion moderate to great (median A/L 0.51, range 0.39-0.58). Surface sculpture as in *C. (C.) mexicana,* except that posterior dorsal area is more distinct, and growth rings are sometimes deep and rather regularly spaced. Lunule, ligament, musculature, dentition, and other internal features as in *C. (C.) mexicana,* except right anterior cardinal is usually reduced.

*Types.* — Montagu's molluscan collections are in the British Museum (Natural History) and the Exeter Museum (Dance, 1966). Fischer-Piette (1942, pl. 15, fig. 11) figured Adanson's specimen of *"le jagon"*, which is in the Muséum nat. d'Hist. nat., in Paris. Clench and Turner (1950) figured C. B. Adams' molluscan types in the Museum of Comparative Zoology (Harvard). The specimens on which Dall (1901b) based his varieties of *C. (C.) orbiculata* are in the National Museum of Natural History.

*Material.* — The phenetic study was based on about 35 Recent specimens from Florida, Bermuda, the Bahamas, and Jamaica; and on about 10 Pleistocene specimens from Bermuda and Florida. All are deposited in the Yale Peabody Museum.

*Discussion.* — Dall (1901b) considered *Codakia (Ctena) orbiculata* to be conspecific with Adanson's Senegalese "*Pectunculus, le jagon*". Lamy (1920) and Chavan (1937) believed that Adanson's species is synonymous only with Dall's *orbiculata* "var." *orbiculata.* If Adanson's species is in fact conspecific with some or all the eastern North American and Caribbean forms referred to *orbiculata,* the first valid binomial name would be *Venus eburnea* Gmelin, 1791 (not to be confused with *Lucina eburnea* Reeve, 1850, a *Divaricella*). Gmelin explicitly referred to Adanson's *"jagon"* in his description of *V. eburnea.* Dall (1901b) stated that *Venus orbiculata* Montagu, 1808, was based on "an adventitious specimen supposed to be British". Pending examination of the original material of all the authors whose names are involved in the synonymy of the species, I prefer not to change the well-known name *orbiculata.*

Dall (1901b) recognized four varieties of *orbiculata.* The "variety" *imbricatula,* proposed as *Lucina imbricatula* by C. B. Adams (1845), was distinguished from *orbiculata s. s.* by having radial ribs which do not bifurcate, and an imbricating appearance of the shell exterior (produced by deep and rather regularly spaced growth rings). The "variety" *filiata* Dall has finer sculpture and non-bifurcating radials, and *recurvata* Dall is more inflated than *orbiculata s. s.* These differences seem analogous to those which Dall employed to differentiate the West Coast species discussed under *C. (C.) mexicana.*

### ?Subgenus **CLAIBORNITES**

*Author.* — Stewart, 1930, pp. 37, 183.

*Types species.* — *Lucina symmetrica* Conrad, 1833c, p. 40, by original designation.

*Discussion.* — Stewart (1930) proposed the name *Claibornites* for *Lucina symmetrica* Conrad (= *L. rotunda* Lea), from the upper middle Eocene Gosport Sand of Alabama. At the same time he proposed two subgenera of *Claibornites: Saxolucina,* type species *Lucina saxorum* Lamarck, 1806; and *Codalucina,* type species *Lucina uncinata* Defrance, 1823. The type species of these subgenera are from the middle Eocene and the Paleocene, respectively, of France.

Chavan (1937) synonymized *Claibornites* with *Epilucina* Dall, 1901b, which was originally proposed as a section of *Callucina;* he treated *Epilucina* as a subgenus of *Codakia,* and synonymized *Saxolucina* and *Codalucina,* which he considered closely related to *Miltha.* More recently, however, he recognized that *Claibornites* and *Epilucina* are generically distinct, but he still treated *Epilucina* as a subgenus of *Codakia;* he placed *Claibornites* in the subfamily Milthinae (Chavan, 1969). *Epilucina* is here considered probably most closely related to *Myrtea.* Some of the larger, more rounded individuals of *E. californica* (the type of *Epilucina*) do bear a certain superficial resemblance to *Claibornites symmetricus,* but the ligament and musculature of the two species are different (see the discussion of *Epilucina* for more details). *Claibornites* as originally defined does, however, seem to have its closest affinities with *Codakia.*

*Diagnosis.* — Shell of medium size, round to higher than long, moderately inflated, anterior expansion small. Surface sculpture distinct, concentric, with growth rings usually formed only near ventral margin. Anterior dorsal area distinct, posterior one faint. Lunule long, wide, triangular, slightly asymmetrical, deep. Ligament deeply inset. Anterior adductor scar long, narrow, straight, parallel to pallial line; posterior adductor scar elliptical. Anterior pedal retractor scar separate from adductor, posterior one not evident. Hinge plate wide, with anterior and posterior laterals single in right valve, double in left; two cardinals in each valve, right anterior cardinal somewhat reduced, right posterior cardinal slightly bifid. Pallial blood vessel scar present. Inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — The type species is the only North American species which can be unequivocally assigned to this subgenus. It was described from the upper middle Eocene Gosport Sand of Alabama; Harris (1897) also recorded a similar, if not identical form, from the early Eocene Hachetigbee Formation of Alabama. *Lucina claytonia* Harris, 1896, from the early Paleocene Clayton Formation of Alabama, resembles *Claibornites symmetricus* in the inconspicuous dorsal areas, long and narrow anterior adductor scar, presence of several growth rings near the ventral margin, and inset ligament; it lacks lateral teeth. Stewart (1930) suggested that this species might belong to *Codalucina*. A West Coast species, *Lucina diegoensis* Dickerson, 1916, from the late Eocene Tejon State of San Diego County, California, was tentatively included in *Claibornites* by Stewart. The shell interior of this species is unknown.

*Lucina concentrica* Lamarck, 1806, from the Eocene of the Paris Basin, was one of Stewart's original species of *Claibornites*, and Chavan (1937) agreed that it closely resembles *C. symmetricus*. *Lucina argentea* Reeve, 1850, from the Moluccas, which Stewart believed to be a probable Recent representative of *Claibornites*, was placed by Chavan (1937) in *Lucinoma*. Reeve did not figure the interior of the shell, and I have not seen specimens of the species. The conspicuous dorsal areas of the specimen in Reeve's figure indicate a possible relationship to *Phacoides* or *Plastomiltha*.

*Lucina cedrensis* Stanton, 1920, from the Fox Hills Formation (Upper Cretaceous, Maestrichtian) of South Dakota and the Cannonball Formation (Paleocene) of North Dakota and South Dakota, may be the earliest North American representative of *Claibornites*. Cvancara (1966) placed this species in *Plastomiltha*, also comparing it to *Codalucina uncinata* (Defrance, 1823). Cvancara stated, however, that the presence of lateral teeth, the anterior ones being strongest, differentiated *L. cedrensis* from *Codalucina uncinata* and from *Plastomiltha claibornensis* (Conrad, 1865b). Speden (1970) tentatively referred *L. cedrensis* to *Epilucina* (*sensu* Chavan, 1937). The most notable difference between *C. symmetricus* and *L. cedrensis* is the shorter, broader anterior adductor scar of the latter.

The generic affinities of *Claibornites* are ambiguous. The deeply inset ligament and the lack of radial sculpture are consistent with assignment to *Miltha*, whereas the nature of the ligament and the presence of lateral teeth are characteristic of *Codakia*. The pedal musculature, with the anterior but not the posterior retractor scar being evident, is like that of *Ctena*. The long, narrow, straight anterior adductor is a character shared with subgenera of both *Lucina (Phacoides)* and *Miltha (Lucinoma, Plastomiltha)*.

Chavan (1969) considered *Claibornites, Codalucina, Saxolucina,* and *Plastomiltha* members of the subfamily Milthinae. His treatment of the Lucinidae in the *Treatise on Invertebrate Paleontology* follows his earlier arrangement in placing *Epilucina* as a subgenus of *Codakia,* but his drawing of the interior of the shell of *E. californica* (fig. E3, 13a, 13b) more closely resembles a species such as *Claibornites*? *cedrensis*. I consider both his earlier and later interpretations of *Claibornites* and *Epilucina* to be based on misinterpretations but do follow his earlier judgment in provisionally assigning *Claibornites* to *Codakia*.

If *Claibornites* is an early branch of the *Codakia* lineage, it is not obviously ancestral to any other subgenus. The earliest probable representatives of *Claibornites* and *Ctena* appear almost simultaneously in the record, the first in the Western Interior and the second in the Gulf Coast area of the United States. The similarity in sculpture and musculature of *Codakia s. s.* and *Ctena,* and the resemblance between the adults of *Ctena* and juveniles of *Codakia s. s.* have been adduced as evidence that *Codakia s. s.* is descended from *Ctena*. Conversely, the similarities between *Claibornites* and *Codakia s. s.* in ligaments and in adult size and shape may indicate a closer relationship between these two taxa. Possibly both *Claibornites symmetricus* and the Paleocene *Codakia*? *gravesi* (Deshayes), which Chavan (1937) considered the earliest representative of *Codakia s. s.,* are related to *Claibornites*? *cedrensis*. The Recent Australian subgenus *Epicodakia* also possesses an inset ligament which does not efface the posterior laterals; its sculpture is much like those of *Codakia s. s.* and *Ctena*.

Not having seen specimens of the European type species of *Saxolucina* and *Codalucina,* I have not attempted to evaluate their phylogenetic position in any detail. If they are indeed most closely related to *Claibornites,* but also similar to subgenera here included in *Miltha,* the *Codakia* and *Miltha* lineages recognized here perhaps should be considered as more nearly related than the taxonomic treatment adopted here makes them appear. Chavan's (1937, 1938) discussion of Late Jurassic Lucinidae, however, indicates that the two lineages were distinct at least that early.

### **Codakia? (Claibornites) symmetrica** (Conrad)

Plate 32, figures 8-10

*Lucina symmetrica* Conrad, 1833c, p. 40; ? Harris, 1896, p. 263, pl. 20, fig. 1.
*Claibornites symmetricus* (Conrad), Stewart, 1930, p. 183.
*Lucina rotunda* Lea, 1833, p. 56, pl. 1, fig. 28; Harris, 1919, p. 122, pl. 40, figs. 1, 2.
*Phacoides (Cavilucina) rotundus* (Lea), Dall, 1903, p. 1364.
*Claibornites rotundus* (Lea), Stewart, 1930, p. 183.

*Codokia (Epilucina) rotunda* (Lea), Chavan, 1937, p. 275.
*Epilucina rotunda* (Lea), Palmer and Brann, 1965, p. 141.
? *Epilucina* sp. Palmer and Brann, 1965, p. 141.
*Claibornites (Claibornites) rotunda* (Lea), Chavan, 1969, p. N502.

*Description.* — Dimensions of one measured specimen as follows: height 33 mm, H/L 1.03, D/L 0.25, A/L 0.43. Shell of medium size, thick. All characters of species as in generic diagnosis.

*Types.* — The types of both Conrad's and Lea's specimens are in the Academy of Natural Sciences of Philadelphia. *Lucina symmetrica* is represented by seven valves, listed by E. J. Moore (1962) as "probable syntypes" (ANSP 30522). Harris (1919) designated as lectotype of *L. rotunda* a left valve, ANSP 5152.

*Material.* — Only a single specimen, from the Gosport Sand of Alabama, was available in the Yale Peabody Museum collections to represent *Claibornites symmetricus* in the phenetic study. Subsequent examination of Conrad's and Lea's types confirmed the diagnosis and description based on this specimen.

*Discussion.* — In the discussion of *Lucina (Cavilinga) pomilia* I have explained why Conrad's names of 1833 have priority over those proposed by Lea in the same year. Dall (1903) rejected Conrad's name on the ground that the species was unrecognizable from Conrad's description. Stewart (1930) used *Lucina rotunda,* but stated that he believed Conrad's description of *L. symmetrica* to be recognizable. Because the types of both species are extant, there is no reason for rejecting Conrad's name. Conrad's and Lea's specimens in the Philadelphia Academy seem clearly to be conspecific.

Palmer and Brann (1965) believed the early Eocene shell identified by Harris (1896) as *Lucina symmetrica* to represent a different species, but I consider the original of Harris's figure (PRI 225) to be conspecific with the middle Eocene forms described by Conrad and Lea.

### Genus **MILTHA**

### Subgenus **MILTHA**

*Milthoidea* Marwick, 1931, p. 70.

*Author.* — H. and A. Adams, 1853, p. 468.

*Type species.* — *Lucina childrenae* Gray, 1825, p. 136, by monotypy. Vokes (1969a) pointed out that this name should be given a feminine termination.

*Diagnosis.* — Shell of medium to large size, higher than long, flat to moderately inflated, sometimes inequivalve, anterior expansion moderate. Surface sculpture concentric, sometimes with faint radials. Growth rings irregularly spaced. Dorsal areas distinct to conspicuous. Lunule generally long, narrow, triangular to oval. Ligament external or slightly inset. Anterior adductor scar long, straight, parallel to pallial line, narrow dorsally but broad ventrally; posterior adductor scar elliptical. Anterior pedal retractor scar separate, posterior one partly separate or not evident. Hinge plate wide; no lateral teeth; two strong cardinals in each valve; right posterior cardinal slightly bifid. Pallial blood vessel scar present. Inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — There are a number of Tertiary species, but the subgenus seems to be rare, both in number of species and in number of individuals, in the Recent fauna. The two Recent species are *Miltha (Miltha) childrenae* (Gray, 1825), from Brazil, and *M. (M.) xantusi* (Dall, 1905), from Baja California. Durham (1950) reported *M. (M.) xantusi* from the Pleistocene of Baja California. Grant and Gale (1931) synonymized *M. (M.) joannis* (Dall, 1905), from the Pliocene of the same region, with *M. (M.) xantusi.* An inequivalve Pliocene species from the Caloosahatchee Formation of Florida, *M. (M.) caloosaensis,* resembles the Recent *M. (M.) childrenae.* Vokes (1969a) separated larger specimens originally assigned to *caloosaensis* as *M. (M.) carmenae.* A form from the Pliocene of New Zealand, *Milthoidea* Marwick, 1931, is probably to be synonymized with *Miltha s. s.* (Chavan, 1938, 1969).

Dall (1903) described two species of *Miltha s. s., M. (M.) chipolana* and *M. (M.) heraclea,* from the middle Miocene Alum Bluff Group of Florida; Gardner (1926) later synonymized them. An early and middle Miocene species from southern California, *M. (M.) sanctaecrucis* (Arnold, 1909) was synonymized with *M. (M.) xantusi* by Grant and Gale (1931). Arnold's type specimen is articulated and the valves are cemented together by matrix, but a specimen which Stewart (1946) identified as *sanctaecrucis* has typical *Miltha s. s.* dentition and musculature. An early Miocene species from the Montera Formation of Peru, *M. (M.) pacifica* Olsson, 1932, resembles species of *Miltha* in size, shape, and sculpture, but no internal features are known.

Dall (1915) noted the presence in the early Miocene Tampa Limestone of a specimen resembling *M. (M.) heraclea* (Dall). This and another specimen from the late Oligocene Suwanee Limestone of Florida were called *Miltha* aff. *M. chipolana* by Mansfield (1937). Another Suwanee species, *Phacoides (Miltha?) hernandoensis* Mansfield, 1937, probably should be referred to *Lucina (Lucina) wacissana* (Dall, 1903).

*M. (M.) perovata* (Dall, 1916), from the late Oligocene Flint River Formation of Georgia; *M. (M.) woodi* (Olsson, 1932), from the late Eocene and middle Oligocene of Peru (type horizon: Talara Formation, late Eocene); and a species from the late Eocene Ocala Limestone of Florida identified by Richards (1953) only as "lucinoid" all seem to belong to *Miltha s. s.* [Vokes (1969a) considered *woodi* an *Eomiltha.*]

Stewart (1930) referred *Dosinia gyrata* Gabb, 1864, from the Eocene of California (precise locality and horizon unknown) to *Miltha (Eomiltha)*, but the specimen figured by Stewart (ANSP 4469) more closely corresponds in shape and sculpture to *Miltha s. s.* No internal features are known, however, and the species may not even be a lucinoid. A middle Eocene species from the Domengine Eocene of California, *Lucina packi* Dickerson, 1916, may belong to *Eomiltha* or to *Miltha s. s.* (Vokes, 1939, 1969a). Another problematic form is *Phacoides quintamaia* Gardner, 1945, from the middle Eocene Yegua Formation of Nuevo Léon, Mexico. Known only from an internal mold too poorly preserved to show dentition or musculature, this species resembles *Miltha s. s.* in general outline but is much smaller (length 20 mm, height 22 mm) than most species of the subgenus. *Phacoides (Miltha?) albaripa* Gardner, 1935, from the early Paleocene Kincaid Formation of Texas, is known only from an articulated specimen; even its assignment to the Lucinacea is questionable.

*Lucina turneri* Stanton, 1896, a California species whose age Stewart (1930) gave as Paleocene and which he tentatively placed in *Codalucina*, is represented in the National Museum of Natural History collections by two syntypes, USNM 108971. The larger, a right valve (L 52 mm, H 49 mm, A 22 mm), shows no internal features. The smaller, an internal mold (L 37 mm, H 34 mm, A 14 mm), is less strongly inflated than the larger specimen, and has musculature and dentition like those of *Miltha s. s.* (with a possible trace of an anterior lateral in the right valve). The syntypes of *L. turneri* may represent two different species.

Like *Lucina s. s., Miltha s. s.* seems to have persisted throughout the Tertiary with very little morphological change. A number of groups seem to have been derived from it, changing the pattern of dentition little but showing a wide variation in musculature and a lesser amount of change in surface sculpture.

Chavan (1938) traced the ancestry of *Miltha s. s.* to *Recticardo*, a principally Paleocene group whose type species, *R. rutoti* Cossmann, 1908, is from the early Paleocene (Montian) of Belgium. The type species differs from most species of *Miltha s. s.* in its smaller size (length and width about 20 mm), more rounded form, strongly bifid cardinals, shorter and narrower anterior adductor, and traces of laterals. Chavan (1938) considered *Recticardo* to have been derived from an Upper Jurassic species, *Mesomiltha pulchra* (Zittel and Goubert, 1861).

### **Miltha (Miltha) xantusi** (Dall)

Plate 33, figures 1-3

*Phacoides (Miltha) childreni* Carpenter, 1864b, pp. 552, 620; Dall, 1901b, p. 812 [*non Lucina childrenae* Gray, 1825].
*Phacoides (Miltha) xantusi* Dall, 1905, p. 111; Lamy, 1920, pp. 121-122.
*Lucina (Miltha) xantusi* (Dall), Grant and Gale, 1931, pp. 291-292, pl. 14, figs. 20a, b.
*Miltha (Miltha) xantusi* (Dall), Chavan, 1938, p. 66; Keen, 1958, p. 98, fig. 198; Durham, 1950, p. 77, pl. 19, figs. 3, 8.
*Miltha xanthusi* [error] (Dall), Olsson, 1961, p. 215, pl. 30, fig. 4.

*Description.* — Shell large to very large (median length of four specimens 60 mm, range 40-94 mm), higher than long (median H/L 1.06, range 1.00-1.09), flat (median D/L 0.14, range 0.14-0.23), anterior expansion moderate (median A/L 0.47, range 0.46-0.47), equivalve. Surface sculpture predominantly concentric, with fine radial striae; growth rings irregularly spaced. Periostracum thin, brown, patchy. Lunule narrow, short, triangular, shallow, asymmetrical (mostly on right valve), more oval on larger specimens. Ligament inset, but not so deeply as in *Codakia.* Anterior adductor scar very long, narrow dorsally and wide ventrally, clublike in shape (Pl. 33, fig. 2), straight, parallel to pallial line; posterior adductor scar oval; anterior pedal retractor separate and posterior one partly separate from adductors. No laterals; two strong cardinals in each valve; right posterior cardinal slightly bifid; hinge plate wide. Pallial blood vessel scar present. Inner ventral margin smooth.

*Types.* — Two bivalved specimens (USNM 5383) in the National Museum of Natural History are labeled "types". The type locality is Cape San Lucas, Baja California. These specimens are figured in Plate 33, figures 1 to 3.

*Material.* — The phenetic study was based on six specimens, including the two syntypes, all in the National Museum of Natural History. All are Recent, from Baja California and the Gulf of California.

*Discussion.* — Dall (1901b) originally believed this species to be identical with *Lucina childrenae* Gray, 1825, the type species of *Miltha.* He considered the type locality, Brazil, given for Gray's species to be erroneous. Subsequently (Dall, 1905), he recognized that two species were involved and proposed the name *Phacoides (Miltha) xantusi* for the West Coast form. The specimen in Plate 33, figure 2, on which the words "*Miltha childreni*" are written, is probably one of those which were before Dall when he prepared the 1901 paper.

Both *M. (M.) childrenae* and *M. (M.) xantusi* seem to be rare. *M. (M.) childrenae,* like the Pliocene *M. (M.) caloosaensis* and the Miocene *M. (M.) chipolana* and *M. (M.) carmenae,* generally has one valve considerably more strongly inflated than the other, but *M. (M.) xantusi* is equivalve. *Miltha s. s.* is the only lucinid subgenus in which inequivalveness has been reported, and apparently its early Cenozoic representatives were equivalve. Unlike other inequivalve taxa, in *Miltha s. s.* either the right valve or the left may be the flatter one in individuals of the same species (Vokes, 1969a). It is not known whether the inequivalve species of *Miltha s. s.* are epifaunal or infaunal. If they are epifaunal, one would predict that they lie on the more convex valve. Stanley (1970, p. 90) stated that "among reclining species that rest on one valve at the substratum surface, a convex lower valve is often employed to maintain the commissure above the substratum and free from clogging. . . . The upper valve of reclining species is nearly always flattened to reduce its resistance to currents, for increased stability." In this case the valves would probably be slightly open all around the free margins of the shell, and the unusual length and breadth of the anterior adductor may reflect its function as a barrier diverting detrital particles from the mouth.

Vokes (1969a), however, noted that, among a collection of 450 valves of several species of *Miltha s. s.,* only 33 had been bored by predators, and only one of the bored valves was a flat one. He surmised that these inequivalve lucinids had lived fairly deeply buried and had lain on the flatter valve, so that they were rarely encountered by predators, and those which were, had been attacked on the valve closer to the sediment surface. It is difficult to visualize how these large inequivalve animals could burrow; perhaps the young individuals assume a position from which they do not subsequently move. The compressed form of such equivalve representatives of the subgenus as *M. (M.) xantusi* certainly seems well suited to burrowing.

### Subgenus **EOMILTHA**

*Author.* — Cossmann, *in* Cossmann and Peyrot, 1911, p. 269.

*Type species.* — *Lucina contorta* Defrance, 1823, p. 274, by original designation.

*Diagnosis.* — Shell of medium to large (possibly extremely large) size, longer than high, flat, anterior expansion moderate. Surface sculpture concentric, fine, with growth rings irregularly spaced. Dorsal areas faint. Lunule short, wide, triangular, shallow. Ligament short, triangular, deeply inset. Anterior adductor scar very long (reaching almost to midpoint of shell), of normal width, curved, with radius of curvature about same as that of pallial line, so that scar parallels pallial line; posterior adductor scar elliptical; anterior pedal retractor scar separate and posterior one partly separate from adductors. Hinge plate wide; no laterals; two cardinals, about equally strong, in each valve; left anterior and right posterior cardinals strongly bifid. Pallial blood vessel scar present. Inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — Though *Eomiltha* is principally an early Cenozoic subgenus, there is one Recent representative, *Miltha (Eomiltha) voorhoevi* (Deshayes, 1857), from the Mozambique Channel (Chavan, 1938). The latest known appearance of the group in the fossil record is represented by *M. (E.) xustris* (Gardner, 1926) and *M. (E.) scolaroi* Vokes, 1969b, from the middle Miocene Alum Bluff Group of Florida.

The largest lucinid known, *Lucina (Pseudomiltha) megameris* Dall, 1901a, from a limestone of probable late Eocene age in Jamaica, may be an *Eomiltha.* The type specimen is 230 mm high and 235 mm long (Dall, 1901a); it is preserved only as an internal mold, showing no dentition. It has the characteristic long, curved anterior adductor scar of *Eomiltha.* Richards (1953) also reported several specimens of this species, some even larger than the Jamaican type specimen, from the late Eocene Moodys Branch Formation of Florida.

*Phacoides (Miltha) ocalanus* Dall, 1903, from the late Eocene Ocala Limestone of Florida, is also preserved only as internal molds. Its size and anterior adductor scar are similar to those of *Miltha (Eomiltha) pandata* (Conrad, 1833a). Both Stewart (1930) and Chavan (1938) assigned the latter species, from the upper middle Eocene Gosport Sand of Alabama, to *Eomiltha. M. (E.) pandata* seems to be similar to the type species, *M. (E.) contorta* (Defrance, 1823), from the Paleocene of France. Chavan (1938) listed several other Paleocene and Eocene species of *Eomiltha,* and noted two Jurassic and one Cretaceous species which he believed to have affinities with both *Eomiltha* and *Recticardo,* the probable ancestor of *Miltha s. s.*

### **Miltha (Eomiltha) pandata** (Conrad)

Plate 33, figures 4-7

*Lucina pandata* Conrad, 1833a, p. 343; Harris, 1919, p. 121, pl. 39, figs. 6, 7.
*Phacoides (Miltha) pandatus* (Conrad), Dall, 1903, p. 1374.
*Miltha (Eomiltha) pandata* (Conrad), Stewart, 1930, p. 191.
*Eomiltha pandata* (Conrad), Chavan, 1938, p. 93; Palmer and Brann, 1965, pp. 138-139.
*Lucina compressa* Lea, 1833, p. 55, pl. 1, fig. 27.

*Description.* — Shell of medium to large size (median length of 23 specimens 36 mm, range 27-46 mm), longer than high (median H/L 0.88, range 0.80-0.97, flat to moderately inflated (median D/L 0.19, range 0.16-0.26), anterior expansion generally moderate (median A/L 0.47, range 0.42-0.56). Surface sculpture concentric, with growth rings irregularly spaced; dorsal areas faint. Lunule short, wide, triangular, shallow, symmetrical or slightly asymmetrical. Ligament deeply inset, resembling that of *Codakia s. s.* Musculature and dentition as in generic diagnosis. Secondary thickening of interiors of most valves emphasizes pallial blood vessel scar. Inner ventral margin smooth.

*Types.* — Conrad's specimens in the Academy of Natural Sciences of Philadelphia, ANSP 30573 (a left valve) and ANSP 30574 (six valves) are listed by E. J. Moore (1962) as "possible syntypes". The holotype of *L. compressa* Lea is ANSP 5194. The specimens figured by Harris (1919) are PRI 763-765.

*Material.* — The phenetic study was based on about 25 specimens, all from the Gosport Sand of Claiborne, Alabama, in the collections of the Yale Peabody Museum. The type specimens listed above were subsequently examined.

*Discussion.* — Harris (1919) stated that this species is the commonest large lucinid in the Gosport Sand, and that it also occurs in the underlying Lisbon Formation. Its assignment to *Eomiltha* is based on its close resemblance to figures of the type species, *Lucina contorta* Defrance, 1823, as given in Deshayes (1824, pl. 16, figs. 1, 2) and to the illustration of the hinge line of *Eomiltha cuvieri* (Bayan) in Cossmann's (1911, p. 269, fig. 128) proposal of the subgenus *Eomiltha.*

### Subgenus **PLASTOMILTHA**

*Author.* — Stewart, 1930, p. 38, 191.

*Type species.* — *Cyclas claibornensis* Conrad, 1865b, p. 146, by original designation.

*Discussion.* — Dall (1903), who considered *Miltha* a subgenus of *Phacoides,* stated that *Miltha* encompassed three distinctive species groups, which he designated A, B, and C. Group B is *Miltha s. s.* and Group C is *Eomiltha* Cossmann, 1911. Stewart (1930) proposed the name *Plastomiltha,* as a subgenus of *Miltha,* for Dall's Group A. The type is a middle Eocene species from Alabama. Some of the later Tertiary species which Dall included in Group A and Stewart in *Plastomiltha* have been placed in *Armimiltha* Olsson and Harbison, 1953. Chavan (1969), however, synonymized *Armimiltha* with *Plastomiltha.*

*Diagnosis.* — Shell of medium to large size, rounded, flat, anterior expansion moderate. Surface sculpture concentric, with two orders of ribs, as in *Lucina (Phacoides);* no growth rings; dorsal areas distinct. Lunule short, wide, triangular, slightly asymmetrical, deep. Ligament external. Anterior adductor scar long, width narrow to normal, straight, parallel to pallial line; posterior adductor scar elliptical. Anterior pedal retractor scar separate from adductor; posterior pedal retractor scar partly separate from adductor, above it but placed toward inside of it rather than directly above it (Pl. 33, fig. 9; compare with *Lucinoma* and *Armimiltha*). Hinge plate wide; no laterals; two cardinals, about equally prominent, in each valve; right posterior cardinal slightly bifid. Pallial blood vessel scar present. Inner ventral margin smooth.

*Distribution and phylogenetic relationships.*—Because I consider Olsson and Harbison's (1953) subgenus *Armimiltha* to be sufficiently distinct from *Plastomiltha* to merit separate status, the only species unquestionably included in *Plastomiltha* is the type species. The Paleocene *Lucina claytonia* Harris, 1896, was believed by Chavan (1938) to link *Saxolucina* and *Plastomiltha* (see discussion of *Claibornites*). Stewart (1930) suggested that *L. claytonia* might belong to *Codalucina,* which Chavan (1969) considered a subgenus of *Claibornites.* It resembles *Miltha (Plastomiltha) claibornensis* in its long, straight anterior adductor, lack of laterals, and general size and shape. It differs in having less conspicuous dorsal areas and concentric ribs which are all equally prominent, with several distinct growth rings near the ventral margin; in these characters it shows closer affinity with *Codakia? (Claibornites) symmetrica* (Conrad, 1833c).

Two other Eocene species may belong to *Plastomiltha.* Harris (1946) described as *Plastomiltha gaufia* a late Eocene species represented by specimens from Alabama, Mississippi, and Louisiana. It differs from *M. (Plastomiltha) claibornensis* in having a more deeply inset ligament and traces of laterals. *Phacoides (Miltha) conventus* Olsson, 1929, from the Eocene Restin Formation of Peru, externally resembles *M. (P.) claibornensis,* but no internal features are known.

The placement of *Plastomiltha* in *Miltha* is based primarily on the flattened shape, the absence of laterals, and the strength of the cardinals. Like both *Miltha s. s.* and several subgenera of the *Lucina* lineage, it has conspicuous dorsal areas. The concentric sculpture and the shape of the anterior adductor are like those of both *Phacoides* and *Lucinoma.* Reasons have been given in the discussion of *Phacoides* for considering it closely related to *Lucina s. s.,* with the similarities to *Plastomiltha* being the result of convergence. It is probable that *Plastomiltha* is closely related, if not ancestral, to *Lucinoma* and *Armimiltha*. (Further evidence is presented in the discussion of these groups.) No species have yet been noted which would be a direct link between *Miltha s. s.*, or the Mesozoic forms considered ancestral to it, and *Plastomiltha*. Possibly *Plastomiltha* is an offshoot from the *Lucina s. s.-Phacoides* lineage in which lateral dentition was lost (cf. Text-fig. 6). Regardless of their ultimate taxonomic fate, however, I consider that *Plastomiltha, Lucinoma,* and *Armimiltha* represent a closely allied group of species.

### **Miltha (Plastomiltha) claibornensis** (Conrad)

Plate 33, figures 8-10

*Cyclas claibornensis* Conrad, 1865b, p. 146.
*Phacoides (Miltha) claibornensis* (Conrad), Dall, 1903, p. 1374, pl. 50, fig. 18.
*Lucina claibornensis* (Conrad), Harris, 1919, pp. 121-122, pl. 39, figs. 8, 9.
*Miltha (Plastomiltha) claibornensis* (Conrad), Stewart, 1930, p. 191.
*Saxolucina (Plastomiltha) claibornensis* (Conrad), Chavan, 1938, pp. 74-76; Chavan, 1969, p. *N*505, fig. E11, 2a, 2b.
*Phacoides (Plastomiltha) claibornensis* (Conrad), Olsson and Harbison, 1953, p. 84, pl. 7, figs. 5, 5a.

*Description.* — Shell of medium to large size (median length of 8 specimens 39 mm, range 25-46 mm), rounded (median H/L 1.00, range 0.91-1.08), flat (median D/L 0.18, range 0.16-0.37), anterior expansion usually moderate (median A/L 0.48, range 0.41-0.53). Variation in height/length ratio may be due to post-depositional distortion. The extreme D/L value of 0.37 is based on a bivalved specimen which is filled by matrix, possibly causing inaccuracy in the measurement. All shell features as described in generic diagnosis.

*Types.* — Syntypes of *Cyclas claibornensis* Conrad, an articulated specimen and a fragment of a left valve, are deposited in the Academy of Natural Sciences of Philadelphia (ANSP 18855). The species was first figured by Dall in 1903; his figured specimen (USNM 90906) is shown in Plate 33, figures 8 and 9. The specimens figured by Harris (1919) are in the Paleontological Research Institution (PRI 766-768).

*Material.* — The phenetic study was based on about 15 specimens, including Dall's figured specimen, from the middle Eocene Lisbon Formation of Alabama; all are in the collections of the National Museum of Natural History. Conrad's type specimens and the specimens figured by Harris were subsequently examined.

*Discussion.* — Conrad's specimens of *Miltha (Plastomiltha) claibornensis* were collected from Claiborne Bluff, Alabama — not from the abundantly fossiliferous Gosport Sand at the top of the bluff, from which most of Conrad's Alabama species were described, but from beds at the base of the bluff. In the older literature, the term "Claiborne sands" generally refers only to the extremely fossiliferous glauconitic sands, about 15-30 feet thick, which are now called the Gosport Sand. The Gosport Sand is a facies of the Lisbon Formation, which ranges from 75 to 165 feet in thickness. The term "Claiborne" is now used in a time-stratigraphic sense; the Claiborne Stage in North America is equivalent to the middle Eocene. The Lisbon Formation, with the Gosport Sand overlying it in western Alabama and interfingering with it in central Alabama, was deposited during the second half of the Claiborne Stage (Toulmin, 1967). The "lower bed at Claiborne Bluff" is thus part of the Lisbon Formation. All the specimens of *M. (P.) claibornensis* which I have seen are from Claiborne Bluff or from beds of equivalent age at Lisbon Bluff, Alabama, except for one specimen (PRI 1082) from Newcastle, Virginia, (age given as middle Eocene, but no specific stratigraphic data furnished).

### Subgenus **LUCINOMA**

? *Gonimyrtea* Marwick, 1929, p. 904, 912.

*Author.* — Dall, 1901b, p. 806.

*Type species.* — *Lucina filosa* Stimpson, 1851, p. 17, by original designation.

*Discussion.* — Dall (1901b) proposed *Lucinoma* as a subgenus of *Phacoides*. Chavan (1938) gave it separate generic status, stating that, although it is in some respects closely analogous to *Miltha*, he considered it most similar to *Myrtea*. He later placed it in his subfamily Myrteinae (Chavan, 1969).

*Diagnosis.* — Shell of medium to large size, longer than high, moderately inflated, anterior expansion small to moderate. Surface sculpture concentric, consisting of lamellar ribs with finer laminae between, dorsal areas faint. Lunule long, wide, triangular, slightly asymmetrical, deep. Ligament external or deeply inset. Anterior adductor scar very long, narrow, straight, parallel to pallial line; posterior adductor scar elliptical. Anterior pedal retractor scar separate and posterior one partly separate from adductors. Hinge plate narrow; no laterals; two cardinals in each valve; right posterior cardinal slightly bifid. Pallial blood vessel scar present. Inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — *Lucinoma* is one of the few lucinids which, at least in the Recent fauna, is most common in cold waters. It has a world-wide distribution. Lamy (1920) listed nine Recent species of *Lucinoma,* from the East Coast and West Coast of North America, the southern tip of South America, Europe, and western Africa. Habe (1958) proposed the name *Alucinoma* for a similar Japanese species. Dall (1901b) stated that the species *Lucinoma aequizonata* (Stearns, 1890) and *Lucinoma heroica* (Dall, 1901b) were dredged from depths of 276 and 1005 fathoms, respectively. No information is given on the depth preferences of the West African species *Lucinoma gaini* (Lamy, 1920); all other species of the subgenus appear to be confined to high latitudes or deep water.

The Recent West Atlantic species *Miltha (Lucinoma) filosa* (Stimpson, 1851), which ranges from Maine to Florida but is found at increasingly greater depths southward (Dall, 1901b), apparently has no fossil record. The closely similar European species *M. (L.) borealis* (Linné, 1767) is found as a fossil from late Miocene time onward (Chavan, 1938). The analogue of these species in western North America, *M. (L.) annulata* (Reeve, 1850), ranges from Alaska to California. Abbott (1954) stated that it is found living at depths from 8 to 75 fathoms, and Valentine (1961) listed it as one of the characterizing species of a Pleistocene association inferred to have inhabited cold waters of the deep inner sublittoral at depths of about 10-25 fathoms. This species is also common in the Californian Pliocene (Grant and Gale, 1931). Grant and Gale considered *M. (L.) acutilineata* (Conrad, 1849) to be synonymous with *M. (L.) annulata*. Conrad's species is abundant in the Miocene of Washington, Oregon, and California (Grant and Gale, 1931; E. J. Moore, 1963). Grant and Gale also considered *M. (L.) hannibali* (B. L. Clark, 1925), from the Oligocene of Washington, to be closely related to *acutilineata* and *annulata*.

*Lucinoma* is represented in the Miocene of the East Coast of the United States by *M. (L.) contracta* (Say, 1824), from the middle Miocene Choptank Formation and Calvert Formation of Maryland. Gernant (1970) interpreted the environment of deposition of the Choptank Formation as "the central and southern regions of a cool temperate marine climate", and stated that *M. (L.) contracta* is most common in those members of the formation which he believed to represent the coolest waters.

Mansfield (1928) described *M. (Lucinoma) contracta murfreesboroensis* from the late Miocene Yorktown Formation of North Carolina. Dall (1903) considered *Lucina subplanata* Conrad, 1841, from the Calvert Formation, a variety of *M. (L.) contracta*.

Several Latin American species have been referred to *Lucinoma*, but, of those of which I have seen specimens, only *M. (L.) chiripanica* (Olsson, 1942), from the late Miocene or early Pliocene of Panama, is sufficiently well preserved to be confidently placed in the subgenus. It most closely resembles the Recent Californian deep-water species *M. (L.) aequizonata* (Stearns, 1890). Two species from middle Oligocene rocks of Ecuador, *M. (L.?) zapotalensis* (Olsson, 1930b) and *M. (L.?) playaensis* (Olsson, 1964) were placed by Olsson in *Lucinoma* (the second only tentatively). The dentition of *zapotalensis* is unknown, and no internal features of *playaensis* are preserved.

Chavan (1938) gave the range of *Lucinoma* in Europe as Miocene to Recent, and stated that he knew of no pre-Oligocene species which definitely belong to *Lucinoma*. He synonymized the Australian Pliocene genus *Gonimyrtea* Marwick, 1929, with *Lucinoma;* but, he later considered *Gonimyrtea* generically distinct from *Lucinoma* and closely related to *Myrtea*. He placed both *Gonimyrtea* and *Lucinoma* in the subfamily Myrteinae (Chavan, 1969). Both *Lucinoma* and *Myrtea* inhabit cold waters and are similarly sculptured; *Myrtea,* however, is considerably smaller than *Lucinoma,* is more elongated anteroposteriorly, and has well-developed lateral teeth and an anterior adductor of normal length and width. *Lucinoma* is similar in size, dentition, shape, and musculature to the Eocene *Plastomiltha,* which I consider probably ancestral to it.

### **Miltha (Lucinoma) filosa** (Stimpson)

Plate 34, figures 1-3

*Lucina radula* Gould, 1841, pp. 69-70 [*non Lucina radula* Montagu, 1803, p. 68, pl. 2, fig. 2].
*Lucina filosa* Stimpson, 1851, p. 17.
*Phacoides (Lucinoma) filosa* (Stimpson), Dall, 1901b, pp. 806, 809, 824, pl. 40, fig. 11; Lamy, 1920, pp. 189-190; Thiele, 1935, p. 866; Abbott, 1954, p. 389, pl. 38j, fig. 78a.
*Lucinoma filosa* (Stimpson), Chavan, 1938, pp. 81, 83.

*Description.* — Shell of medium to large size (median length of 24 specimens 36 mm, range 12-50 mm), longer than high (median H/L 0.90, range 0.83-0.97), moderately inflated (median D/L 0.21, range 0.19-0.27), anterior expansion small to moderate (median A/L 0.44, range 0.37-0.48). Ligament either external or inset in a deep groove (cf. figs. 2 and 3, Pl. 34). All other characters as in generic diagnosis.

*Types.* — Dance (1966) stated that Stimpson's collection, in which the type of *Lucina filosa* was presumably included, was destroyed in the Chicago Fire of 1871. So far as I know, no neotype has been designated.

*Material.* — The phenetic study was based on about 30 specimens, from Massachusetts and Rhode Island, in the collections of the Yale Peabody Museum.

*Discussion.* — As previously stated, this is a cold-water species, ranging from Maine to Florida, but living at greater depths in lower latitudes. Gould (1841) originally misidentified it as *Lucina radula* Montagu, a synonym of *Venus borealis* Linné, the European representative of *Lucinoma*.

### Subgenus **ARMIMILTHA**

*Author.* — Olsson and Harbison, 1953, p. 84.

*Type species.* — *Lucina disciformis* Heilprin, 1887, p. 94, pl. 12, fig. 28, by original designation.

*Discussion.* — Olsson and Harbison (1953) proposed *Armimiltha* as a subgenus of *Phacoides.* They noted that the species which they included in *Armimiltha* had been placed by Dall (1903) in *Miltha* (Group A) and by Stewart (1930) in *Plastomiltha.*

*Diagnosis.* — Shell of large size, generally somewhat longer than high, flat to moderately inflated, anterior expansion usually moderate. Surface sculpture concentric, rugose, with finer concentrics between sharply raised ribs. Dorsal areas distinct. Lunule short, wide, triangular, deep, slightly asymmetrical. Ligament external or deeply inset. Anterior adductor scar very long, narrow, consisting of a short, straight dorsal portion parallel to pallial line, and a long, also straight ventral portion diverging sharply, at slightly more than 90°, from dorsal portion (Plate 34, figure 6). Posterior adductor scar elliptical. Anterior pedal retractor scar not evident; posterior one partly separate from adductor, but inside rather than above it. Hinge plate wide; no laterals; two strong cardinals in each valve, right posterior cardinal strongly bifid. Pallial blood vessel scar present. Inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — *Miltha (Armimiltha) disciformis* is common in the Caloosahatchee Formation and equivalent beds in Florida. The Caloosahatchee has until recently been regarded as Pliocene; at least part of it is now considered probably Pleistocene. *Armimiltha* does not seem to be represented in the Recent fauna.

Olsson and Harbison (1953) placed only two species, *M. (A.) disciformis* and *M. (A.) hillsboroensis* (Heilprin, 1887), from the early Miocene Tampa Limestone of Florida, in *Armimiltha.* In the National Museum of Natural History collections there is also a specimen of *M. (A.) hillsboroensis* from the late Oligocene Flint River Formation of Georgia. *M. (A.) heilprini* (Gardner, 1926), from the middle Miocene Alum Bluff Group of Florida, may be based on weathered and abraded specimens of *M. (A.) hillsboroensis* which have lost most of the rugose lamellae. Gardner stated that there are some differences in the shapes of the lunules and that the middle Miocene forms have a greater height/length ratio. The latter character, however, is variable in *M. (A.) disciformis.*

The surface sculpture and musculature of *Armimiltha* seem sufficiently different from those of *Plastomiltha* to warrant subgeneric separation (but see Chavan, 1969). The surface sculpture of *Armimiltha* can be derived from that of *Plastomiltha* by an increase in the rugosity of the first-order concentric ribs. The posterior pedal retractor scar of *Plastomiltha* is positioned slightly toward the inside of the posterior adductor; further rotation inward would produce the positioning seen in *Armimiltha* (cf. figs. 2, 5, Pl. 34). No anterior pedal retractor scar is discernible. Perhaps the development of the dorsal segment of the anterior adductor, extending high up into the valve, results from fusion of the dorsal part of the anterior adductor with the pedal retractor; in other lucinids, the anterior pedal retractor, when separate from the anterior adductor, lies just above and inside it.

#### **Miltha (Armimiltha) disciformis** (Heilprin)

Plate 34, figures 4-6

*Lucina disciformis* Heilprin, 1887, p. 94, pl. 12, fig. 28.
*Phacoides (Miltha) disciformis* (Heilprin), Dall, 1903, pp. 1374, 1377.
*Miltha (Plastomiltha) disciformis* (Heilprin), Stewart, 1930, p. 191.
*Saxolucina (Plastomiltha) disciformis* (Heilprin), Chavan, 1938, pp. 76-77.
*Phacoides (Armimiltha) disciformis* (Heilprin), Olsson and Harbison, 1953, p. 84, pl. 7, figs. 1, 1a, 1b; DuBar, 1958, p. 167, pl. 6, figs. 3, 7.

*Description.* — Shell of large size (median length of 19 specimens 61 mm, range 28-74 mm), generally longer than high (median H/L 0.96, range 0.92-1.09), flat to moderately inflated (median D/L 0.20, range 0.16-0.26), anterior expansion usually moderate (median A/L 0.46, range 0.42-0.60). Sculpture, lunule, musculature, and dentition as in generic diagnosis. Ligament generally deeply inset, but degree of internalization variable (as in *Lucinoma*). Shell interior often thickened, and dotted by small punctae apparently representing points of mantle attachment. Pallial blood vessel scar present. Inner ventral margin smooth.

*Types.* — Heilprin's original specimens may be in the collection of the Wagner Free Institute of Science in Philadelphia. The specimen figured by Olsson and Harbison is in the Academy of Natural Sciences of Philadelphia (ANSP 570).

*Material.* — The phenetic study was based on about 20 specimens, all from the Caloosahatchee Formation of probable Pliocene age in Florida, in the collections of the National Museum of Natural History and the Yale Peabody Museum. Specimens identified by Olsson and Harbison, in the Philadelphia Academy collections, were subsequently examined.

*Discussion.* — Olsson and Harbison (1953) noted that the concentric sculpture of *M. (A.) disciformis* is regularly spaced and only moderately elevated on the dorsal part of the shell, becoming more irregular and more rugose with age.

The juvenile portion of the shell looks very much like the shell of *M. (Plastomiltha) claibornensis*. I have noted in the discussion of *Miltha s. s.* that the inequivalve species, at least, of this group may have been epifaunal. The rugosity and irregularity of the sculpture of *Armimiltha* may also have been adaptations to an epifaunal habitat in, perhaps, a rather more turbulent area than that inhabited by the smoother-shelled species of *Miltha s. s.* The sculpture of *Armimiltha* is reminiscent of that of taxa such as the oysters and the chamids.

*M. (A.) disciformis* is apparently found only in the Caloosahatchee Formation of Florida. Until recently, following Heilprin (1887), the Caloosahatchee had been regarded as definitely Pliocene in age. DuBar (1958) presented evidence, based mostly on the vertebrate fauna, that the formation was actually Pleistocene (Kansan or younger). He conceded that the molluscan fauna, with 50-60% extinct species, indicated a Pliocene age, but believed that many of the "species" are no more than subspecifically distinct from their Recent relatives, and that none are restricted to deposits of undoubted Pliocene age [though *M. (A.) disciformis* itself is not known to be living].

Several other workers have challenged DuBar's interpretation. In particular, Brooks (1968) showed that the beds assigned to the Caloosahatchee Formation represent a complex sequence of units, including numerous erosional and solutional unconformities. Olsson (1968) suggested a redefinition of the Caloosahatchee, removing from it the unit which DuBar (1958) considered its upper member. The majority opinion among Floridian geologists seems to be that these upper beds may indeed be lower Pleistocene, but that the abundantly fossiliferous marl whose fauna was described by Heilprin (1887) and Dall (1903) is still to be considered Pliocene. I have accordingly referred to the Caloosahatchee as being Pliocene in age throughout this paper.

### Genus **MYRTEA**

#### Subgenus **MYRTEA**

***Myrtaea* Dall, 1901b, p. 804.**

*Author.* — Turton, 1822, p. 183.

*Type species.* — *Venus spinifera* Montagu, 1803, p. 577, by monotypy.

*Discussion.* — The type species of *Myrtea* Turton, 1822, is a Recent British species. Dall (1901b) changed the spelling of the name to *Myrtaea*. This unexplained emendation is not justified under the provisions of the International Code of Zoological Nomenclature (Articles 26-30, 32).

*Diagnosis.* — Shell of very small to medium size, longer than high, generally moderately inflated, anterior expansion moderate. Surface sculpture concentric, of evenly spaced ribs, sometimes with second-order lamellae between them. Concentric ribs reflected into spines at posterior dorsal margin; dorsal areas faint. Lunule long, triangular or oval. Ligament external. Anterior adductor scar of normal length and width, straight, diverging from pallial line; posterior adductor scar round. Anterior pedal retractor scar separate and posterior one partly separate from adductors. Hinge plate narrow, with one cardinal in right valve, two in left; anterior and posterior laterals single in right valve, double in left; laterals sometimes obsolescent. Pallial blood vessel scar absent. Inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — The Recent type species of *Myrtea s. s.*, *M. (M.) spinifera*, is found in the Mediterranean and in the eastern Atlantic from Norway to the Cape Verde Islands (Lamy, 1920). There is one Recent North American representative of the typical subgenus, *M. (M.) pristiphora* Dall and Simpson, 1901. Recent species of *Myrtea s. s.* have also been described from Australia and Asia (Lamy, 1920; Chavan, 1938). Iredale (1924) proposed the name *Notomyrtea* (type species *Myrtea botanica* Hedley, 1918) for the Australian species.

Pliocene representatives of *Myrtea s. s.* seem to be confined to Europe and perhaps Australia; none have been described from North America. The subgenus is also present in the European Miocene but has no pre-Miocene fossil record in Europe (Chavan, 1938). One species, *M. (M.) limoniana* Dall, 1903, from the middle Miocene Bowden Formation of Jamaica, resembles *M. (M.) pristiphora* in its thin shell and in having closely spaced concentric ribs, all equally prominent. *M. (M.) taylorensis* Mansfield, 1940, from the late Oligocene Chickasawhay Marl, and *M. (M.) vicksburgensis* (Casey, 1903), from the middle Oligocene Vicksburg Group (both formations are in Mississippi), are closely similar to *M. (M.) limoniana*.

As previously stated, some Eocene species formerly assigned to *Myrtea* seem more closely related to *Callucina*. *Lucina bisculpta* Meyer, 1886, from the middle Eocene of Alabama, may belong to *Myrtea*. Harris (1919) believed this species to be related to *Lucina (Callucina) papyracea*, which it resembles in the short, curved anterior adductor and the obsolescence of the lateral teeth. The considerable anteroposterior elongation and the presence of two orders of concentric ribs, however, may indicate relationship to *Myrtea*.

Two species which seem to be closely related, *Phacoides*

*(Lucinisca) mesakta* Gardner, 1935, from the early Paleocene Kincaid Formation of Texas, and *Lucina linearia* Stephenson, 1941, from the late Cretaceous (Maestrichtian) Navarro Group of Texas, were mentioned in the discussion of *Lucinisca.* Both have two orders of concentric ribs, are anteroposteriorly elongate, and have musculature like that of *M. (Myrtea) spinifera.* "*Phacoides*" *mesakta* has well-developed posterodorsal spines at the terminations of the first-order concentrics. Its right-valve dentition is unknown. "*Lucina*" *linearia* has two cardinals in each valve. The denticulation of the inner ventral margin in both species and the additional right-valve cardinal in "*Lucina*" *linearia* are the principal differences between these species and species of *Myrtea s. s.*

It is difficult to determine the origin of *Myrtea.* Chavan (1938) originally considered that both *Myrtea* and *Lucinoma* were probably derived from Tertiary representatives of the Jurassic and Cretaceous *Mesomiltha,* which he also believed to be ancestral to other taxa here placed in *Miltha* and *Anodontia.* As shown above, *Myrtea s. s.* may have existed as early at Late Cretaceous time. Chavan (1946b) subsequently stated that *Myrtea* and *Lucinoma* might be related, through *Mesomiltha,* from the Jurassic to Eocene taxon *Jagonoma,* which he considered probably ancestral to *Ctena.* Chavan in 1969 placed *Mesomiltha* and *Jagonoma* in the subfamilies Myrteinae and Lucininae, respectively. He still believed *Myrtea* and *Lucinoma* to be closely related. The major similarity between them, aside from their preference for cold waters, is their surface sculpture, of a type which, as indicated in the discussions of *Phacoides* and *Plastomiltha,* may have developed independently in more than one lucinid lineage. Also, there are several Tertiary and Recent species which are much like *M. (M.) spinifera* but which lack second-order concentrics.

A possible early species of *Myrtea s. s.* is *Lucina potosina* Castillo and Aguilera, 1895, from the Upper Jurassic Malone Formation of western Texas and correlative beds in northern Mexico [Cragin (1905), Imlay (1940)]; I have not seen specimens of this species, which from the illustrations appear to be poorly preserved.

Chavan (1951b) proposed a new subgenus of *Myrtea, Gardnerella,* with *M. waltonensis* Gardner, 1926, from the middle Miocene Alum Bluff Group of Florida, as type species. The other originally included species, both Eocene, were *Eophysema cossmanni* Chavan, 1941, and *Lucina ozarkana* Harris, 1897. Stewart (1930) considered *L. ozarkana* closely related to *L. subvexa* Conrad, the type species of his subgenus *Eophysema; Eophysema* is probably ancestral to *Anodontia s. s. Myrtea waltonensis* seems to have affinities with species of both *Myrtea* and *Anodontia.* It resembles *Anodontia s. s.* in its strong inflation and its fine concentric sculpture with irregularly spaced growth rings. The hinge of the type specimen is broken, but Gardner (1926) described the species as having one cardinal in each valve, with the "dorsal margins modified to function as laterals". The type specimen is small and elongated (length 8.2 mm, height 7.1 mm). The short, straight muscle scar, which diverges sharply from the pallial line, and the spines on the posterodorsal margin suggest affinity with Myrtea. The anterodorsal margin is straight, not gently concave upward as in both *M. (M.) spinifera* and *A. (Anodontia) alba. M. waltonensis* resembles *A. (Eophysema) subvexa* in its small size and possession of faint radial sculpture, small cardinals, and poorly defined laterals. Chavan in 1969 placed *Gardnerella* in the Myrteinae but considered it generically distinct from *Myrtea.* I consider it likely that *M. waltonensis* is a descendant of one of the Eocene species here assigned to *Anodontia (Eophysema),* in which case *Gardnerella* should be considered a subgenus of *Anodontia* rather than of *Myrtea.* As stated in the discussion of *Eophysema,* similarities in dentition and musculature between species of this subgenus and early species of *Myrtea s. s.* suggest a close relationship between the *Myrtea* lineage and the *Anodontia* lineage.

### **Myrtea (Myrtea) spinifera** (Montagu)

Plate 34, figures 7-10

*Venus spinifera* Montagu, 1803, pp. 577-579, pl. 17, fig. 1.
*Myrtea spinifera* (Montagu), Turton, 1822, p. 133; Lamy, 1920, pp. 217-219, fig.; Chavan, 1938, pp. 85, 86, 88.
*Myrtaea spinifera* (Montagu), Dall, 1901b, p. 804; Dall, 1903, p. 1356.
*Myrtea (Myrtea) spinifera* (Montagu), Thiele, 1935, p. 866; Chavan, 1969, p. *N*500, fig. E6.1, E7, 1a, 1b, 1c.

*Description.* — Shell of medium size (median length of 26 specimens 22 mm, range 12-28 mm), longer than high (median H/L 0.84, range 0.77-0.92), moderately inflated (median D/L 0.22, range 0.20-0.26), anterior expansion generally moderate (median A/L 0.46, range 0.40-0.52). Surface sculpture concentric, distinct, of raised ribs with finer concentric lamellae between. Dorsal areas faint; posterodorsal terminations of first-order concentrics raised into small, sharp spines. Lunule long, wide, oval, shallow, strongly asymmetrical (greater part in left valve). Ligament external. Anterior adductor scar of normal length and width, straight, diverging from pallial line; posterior adductor scar round. Anterior pedal retractor separate and posterior one partly separate from adductors. Hinge plate narrow; anterior and posterior laterals single in right valve, double in left; laterals sometimes obsolescent; one non-bifid cardinal in right valve, two cardinals in left. Shell interior white or yellow; no pallial blood vessel scar; inner ventral margin smooth.

*Types.* — The location of Montagu's specimens of *Venus spinifera* is unknown to me; his collections are in the British Museum (Natural History) and the Exeter Museum, England (Dance, 1966).

*Material.* — The phenetic study was based on about 30 Recent specimens from the British Isles, in the collections of the Yale Peabody Museum and the National Museum of Natural History.

*Discussion.* — According to Lamy (1920), *Myrtea (Myrtea) spinifera* has been found living from Norway to the Cape Verde Islands, off the western coast of Africa. Allen (1958) stated that *M. spinifera* is found in European seas at depths ranging from 4 to 60 fathoms, inhabiting mud and muddy sand.

It is interesting to note that there is apparently no impression on the shell interior of the pallial blood vessel in *M. (Myrtea) spinifera,* nor in *M. (Eulopia) sagrinata* (Dall) and *M. (Myrteopsis?) lens* Verrill and Smith. Allen (1958, fig. 28) indicated the presence of a pallial blood vessel in his figures of the anatomy of *M. (M.) spinifera,* but apparently in these species no trace of pallial blood vessel is produced on the shell interior. In all other lucinid species included in this study, a pallial blood vessel scar is present on at least some of the shells, generally the larger ones. Nothing can be inferred from its not having been seen in *M. (E.) sagrinata,* only three specimens of which were available for study; but about 30 specimens of *M. (Myrtea) spinifera* and about 70 of *M. (Myrteopsis?) lens* showed no evidence of the blood vessel.

Most lucinids which appear to have reached adult size have a secondary deposit of shell material within the pallial line, into which the muscle scars and pallial blood vessel scars are impressed. This deposit may be only a flaky film, as in *Lucina (Lucina) pensylvanica,* or the deposit may be so thick that the muscle and pallial blood vessel scars appear to be sunken into it, as in *L. (Stewartia) anodonta* and *Miltha (Eomiltha) pandata.* The mantle surface in the Lucinidae adheres closely to the shell (Dall, 1903), generally being attached to the shell at regular or irregular intervals, as shown by small dots or punctae on the shell interior. Apparently calcium carbonate being secreted by adult lucinids is used for thickening the shell interior rather than for further growth in height and length. In some cases the pallial blood vessel scar appears as a line across the secondary deposit; in others the scar is marked by small dots, either arranged in a double row or irregularly spaced. In the first case, evidently, the area of the mantle crossed by the pallial blood vessel does not secrete secondary deposits; in the second, attachment of this vessel to the shell interior, either completely or at intervals, produces an indentation which is emphasized by the secondary deposits. Both the degree of development of the secondary deposits and the mode of outlining the pallial blood vessel show considerable intraspecific variation. Secondary deposits seem more prominent in fossil than in Recent individuals, even of the same species; perhaps differences in structure between the various shell layers are emphasized by diagenesis.

Secondary deposits are formed in some individuals of all three of the species of *Myrtea* mentioned above, but there seems to be no trace of attachment of the pallial blood vessel to the shell interior, nor any differential formation of secondary deposits related to the position of the pallial blood vessel scar. *Epilucina californica,* which seems to have its closest affinities with *Myrtea,* does, however, have a pallial blood vessel scar.

### Subgenus **EULOPIA**

*Author.* — Dall, 1901b, p. 804.

*Type species.* — *Lucina sagrinata* Dall, 1886, p. 265, by original designation.

*Discussion.* — Dall (1901) proposed *Eulopia* as a subgenus of *Myrtea.* Chavan (1938) originally considered the name *Eulopia* as probably unnecessary (p. 86), but later in the same paper suggested that the similarity of the Australian Pliocene to Recent subgenus *Notomyrtea* to *Eulopia* indicated that *Eulopia* should have subgeneric if not generic rank (p. 231). He later synonymized *Eulopia* with *Myrtea* and also tentatively synonymized *Notomyrtea* with *Myrtea* (Chavan, 1969).

*Diagnosis.* — Shell of very small size, longer than high, moderately inflated, anterior expansion moderate to great. Sculpture of evenly spaced concentric ribs with short radial lines (vermicular sculpture) between each two concentrics; radials discontinuous, not crossing concentrics. Dorsal areas faint; posterodorsal spines present. Lunule long, narrow, triangular or oval, slightly asymmetrical, shallow. Ligament external. Anterior adductor scar of normal length and width, straight, diverging slightly from pallial line; posterior adductor scar round. Anterior pedal retractor separate and posterior one partly separate from adductors. Hinge plate narrow, with anterior and posterior laterals single in right valve, double in left; one non-bifid cardinal in right valve, two in left. Pallial blood vessel scar not evident. Inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — There are only three known North American species of *Eulopia* — the Recent type species and two middle Miocene species from the Bowden Formation of Jamaica. *Myrtea (Eulopia) vermiculata* Dall, 1903, is nearly identical with *M. (E.) sagrinata. M. (E.) furcata* Dall, 1903, resembles these species in shape, musculature, and dentition but is somewhat larger (length 14 mm vs. 6 to 10 mm for *sagrinata* and *vermiculata*), and the radial sculpture is partly continuous across the concentrics. The Bowden Formation is apparently a shallow-water deposit, but the Recent *M. (E.) sagrinata* is known from waters ranging in depth from 85 to 300 fathoms (Dall, 1901b). Because most Tertiary lucinids have been collected from nearshore deposits, if post-middle Miocene representatives of *Eulopia* were inhabitants of deep waters their absence from the North American fossil record is not surprising.

Dall (1903) placed a middle Eocene species, *Lucina astartiformis* Aldrich, 1897, in *Eulopia. L. astartiformis* has discontinuous radial ribs between raised concentrics and has some posterodorsal spines, but unlike species of *Eulopia* its shape is trigonal rather than elongate, and there are no lateral teeth. The anterior adductor scar is rather short. This species is probably a lucinid, but its generic affinities are uncertain.

Iredale (1924) placed in *Notomyrtea* both a species (the type, *Myrtea botanica* Hedley, 1918) which has radial (apparently vermicular) sculpture in addition to the concentrics, and another (*M. bractea* Hedley, 1911) which lacks radials. Dall (1901b) indicated that another West Pacific species, *Lucina fabula* Reeve, 1850, has affinities with *Eulopia.*

### **Myrtea (Eulopia) sagrinata** (Dall)

Plate 34, figures 11-13

*Lucina sagrinata* Dall, 1886, pp. 265-266; Dall, 1890a, p. 263, pl. 14, fig. 11.
*Myrtaea (Eulopia) sagrinata* (Dall), Dall, 1901b, pp. 804-805.
*Myrtea (Eulopia) sagrinata* (Dall), Lamy, 1920, p. 220; Thiele, 1935, p. 835; Chavan, 1938, pp. 86, 88.
*Myrtea (Myrtea) sagrinata* (Dall), Chavan, 1969, p. *N*499.

*Description.* — Shell of very small size (median length of 3 specimens 6.1 mm, range 5.4-9.8 mm), longer than high (median H/L 0.85, range 0.81-0.92), moderately inflated (median D/L 0.28, range 0.26-0.28), anterior expansion variable (median A/L 0.48, range 0.43-0.54). Surface sculpture as in generic diagnosis; periostracum thin, brown, with discontinuous radials present on both periostracum and underlying shell surface. Lunule long, narrow, triangular, slightly asymmetrical (greater part on left valve), shallow. Ligament, musculature, dentition, and other internal features as in generic diagnosis. Muscle scars poorly impressed; in the type specimen, thin secondary deposits have apparently been laid down and later partly flaked off, obscuring the boundaries of the pallial line and muscle scars (Plate 34, figures 12, 13).

*Types.* — The holotype of *Myrtea (Eulopia) sagrinata,* figured in figures 11 to 13 of Plate 34, is in the National Museum of Natural History (USNM 64277). It is probably the specimen figured by Dall in 1890.

*Material.* — The phenetic study was based on three Recent specimens, including the type specimen, from the Gulf of Mexico and the Caribbean; all are in the collections of the National Museum of Natural History.

*Discussion.* — Dall (1901b) reported that the habitat of this species is the "Florida Keys and westward to Yucatan Strait, in 85 to 300 fathoms".

### Subgenus **MYRTEOPSIS**

? *Levimyrtaea* Olsson, 1964, p. 51.

*Author.* — Sacco, 1901, p. 96.

*Type species.* — Probably *Myrtea (Myrteopsis) magnotaurina* Sacco, 1901, p. 96, pl. 21, figs. 32-36 (see discussion below), by monotypy.

*Discussion.* — Sacco (1901) proposed the name *Myrteopsis,* as a subgenus of *Myrtea,* for species from the Italian Miocene which differed from *M. (Myrtea) spinifera* in their greater size, almost smooth surface, lack of posterodorsal spines, and virtual or complete lack of teeth. He stated that the type species of this subgenus was "*M. taurolaevis*". As Dall (1903) pointed out, however, Sacco gave no reference to this species, nor did he describe or figure it. The only species described and figured under *Myrteopsis* was *M. magnotaurina* (reference given above). Unless a prior use of the name *M. taurolaevis* can be found, it must be regarded as a *nomen nudum,* mentioned but not accompanied by a "description, definition, or indication" (International Code of Zoological Nomenclature, Art. 12). *M. magnotaurina* would then be the type species of *Myrteopsis* by monotypy. Conversely, Chavan (1969) stated that the type species of *Myrteopsis* is "*M. taurolaevis (= M. magnotaurina)*", by original designation.

*Diagnosis [adapted from Sacco (1901) and Woodring (1925)].* — Shell of medium to large size, longer than high, moderately inflated, anterior expansion moderate to great. Surface sculpture fine, concentric, no second-order lamellae, growth rings irregularly spaced. Dorsal areas faint, with no posterodorsal spines. Lunule long, narrow, shallow. Ligament deeply inset. Hinge with one cardinal in right valve, two in left; cardinals obsolescent and laterals absent or obsolescent. Musculature unknown.

*Distribution and phylogenetic relationships.* — *Myrtea (Myrteopsis) magnotaurina* Sacco, 1901, is from the middle Miocene (Helvetian) of the Turin Hills, northern Italy. Woodring (1925) placed *Codakia (Ctena) pertenera* (Dall, 1903) from the Helvetian Bowden Formation of Jamaica, in *Myrteopsis;* but I have given reasons in the discussion of *Ctena* for accepting Dall's original subgeneric assignment of this species.

Olsson (1964) proposed *Levimyrtaea* as a subgenus of *Myrtea*. The type species is *M. (L.) inconspicua* Olsson, 1964, from the late Miocene or early Pliocene Esmeraldas Formation of Ecuador. The type species is somewhat smaller than *M. (Myrteopsis) magnotaurina* — Sacco gave the ranges of length and height, respectively, of his species as 25 to 42 mm and 18 to 32 mm; the holotype of *M. inconspicua* is 8.6 mm long and 8.1 mm high. In shape and surface sculpture, *Myrteopsis* and *Levimyrtaea* are similar; in both taxa, also, the cardinal and lateral teeth are obsolete. In neither group is the musculature known; the shell interior of *M. (L.) inconspicua* is accessible, but the muscle scars are too faintly impressed to permit discernment of their size and shape. *M. (L.) inconspicua* has traces of discontinuous radials on part of the shell.

"*Myrtea*" *lens* (Verrill and Smith, *in* Verrill, 1880a), discussed below, is identical externally with *M. (L.) inconspicua;* the hinge teeth of *M. lens* are completely lacking, except for traces of a single right-valve cardinal in a few individuals. *Myrteopsis magnotaurina*, *Levimyrtaea inconspicua*, and "*Myrtea*" *lens* were probably derived from *Myrtea s. s.*, with the surface sculpture becoming finer, with loss of the second-order concentrics, and with the dentition becoming gradually effaced. I have no information on the habitat of *Myrteopsis magnotaurina*, but both *Levimyrtaea inconspicua* and "*Myrtea*" *lens* are found in deep-water muds (Olsson, 1964; Verrill, 1880a, 1880b; Dall, 1901b). "*Myrtea*" *lens* has here been tentatively assigned to *Myrteopsis* in the expectation that further study will show *Myrteopsis* and *Levimyrtaea* to be synonymous. Some differences between *Myrteopsis magnotaurina* and *M.*? *lens* (dorsal areas, spinosity, ligament) are evident from comparing the diagnosis of *Myrteopsis* and the description of *M.*? *lens*.

### **Myrtea (Myrteopsis?) lens** (Verrill and Smith)

Plate 34, figures 14-16

*Loripes lens* Verrill and Smith, *in* Verrill, 1880a, p. 400; Verrill, 1880b, p. 400.
*Myrtaea lens* (Verrill and Smith), Dall, 1901b, p. 804.
*Myrtea lens* (Verrill and Smith), Lamy, 1920, p. 220.
? *Loripes compressa* Dall, 1881, p. 135; Dall, 1886, p. 266; Dall, 1889, p. 72, pl. 14, fig. 2.
? *Myrtaea compressa* (Dall), Dall, 1901b, p. 804.
? *Myrtea compressa* (Dall), Lamy, 1920, p. 220.

*Description.* — Shell thin, small (median length of 32 specimens 12 mm, range 8-15 mm), longer than high (median H/L 0.93, range 0.87-1.00), moderately inflated (median D/L 0.22, range 0.19-0.27), anterior expansion usually moderate (median A/L 0.45, range 0.33-0.55). Surface sculpture concentric, fine, with irregularly spaced growth rings. Dorsal areas distinct; posterodorsal spines present but less regularly developed than in *M. (Myrtea) spinifera;* periostracum brown, covering entire shell exterior. Lunule long, narrow, triangular, slightly asymmetrical, deep. Ligament external. Anterior adductor scar of normal length and width, straight, parallel to pallial line in most individuals but diverging from it in some. Posterior adductor scar elliptical; anterior pedal retractor scar separate and posterior one partly separate from adductors. Hinge plate narrow, hinge edentulous or with traces of a single cardinal in right valve. Pallial blood vessel scar absent. Inner ventral margin smooth.

*Types.* — Apparently no lectotype has been designated for this species. It was first collected by the U.S. Fish Commission's survey of the fauna of the New England coast. Most of the material to which Verrill and Smith gave the name *Loripes lens* is in the invertebrate zoology collections of the Yale Peabody Museum. In addition, there are about 20 specimens bearing a U.S. Fish Commission locality number in the Recent type collection of the National Museum of Natural History (USNM 64270). Other species in this collection have the word "type" on their labels; the specimens of *Myrtea (Myrteopsis?) lens* in the National Museum type collections, however, are not explicitly labeled as types.

*Material.* — The phenetic study was based on about 50 Recent specimens in the Yale Peabody Museum and about 20 in the National Museum of Natural History, all from Cape Cod or Rhode Island.

*Discussion.* — Dall (1901b) stated that this species is found "from Cape Cod, Massachusetts, south to the Antilles and Rio de Janeiro, Brazil, in 50 to 464 fathoms, bottom temperatures ranging from 41.5° to 46.5°F.". In 1901 Dall tentatively synonymized the deep-water West Indian species *Myrtea compressa* (Dall, 1881) with *Myrtea lens*, believing it to be only a more "transverse and compressed variety" of the latter.

### ?Subgenus **EPILUCINA**

*Author.* — Dall, 1901b, p. 806.

*Type species.* — *Lucina californica* Conrad, 1837, p. 255, pl. 20, fig. 1, by monotypy.

*Discussion.* — Dall (1901b) proposed *Epilucina* as a section of *Callucina,* one of his subgenera of *Phacoides.* Chavan (1937) showed that several features, notably the strongly asymmetrical lunule, smooth inner ventral margin, and presence of laterals, distinguished *Epilucina* from *Callucina.* He made *Epilucina* a subgenus of *Codakia,* synonymizing *Claibornites* Stewart, 1930, with it. Though the type species of *Epilucina* and *Claibornites* have the same sort of concentric sculpture, and some of the more rounded individuals of *E. californica* are thus externally similar to *Claibornites symmetricus,* the two species are sufficiently different that considering them consubgeneric seems unjustifiable. Notably, *C. symmetricus* has a deeply inset ligament, a long, narrow anterior adductor, and a lunule which is only slightly asymmetrical. In *E. californica,* the ligament is external, the anterior adductor of normal size, and the lunule strongly asymmetrical. Too, *C. symmetricus* is generally round or slightly higher than long, while *E. californica* is moderately to strongly elongate. For these reasons I have rejected Chavan's synonymization of *Claibornites* and *Epilucina.* Reasons for the placement of *Epilucina* in *Myrtea* are discussed below.

*Diagnosis.* — Shell of medium size, longer than high, moderately inflated, anterior expansion moderate. Surface sculpture concentric, coarse, with irregularly spaced growth rings. Anterior dorsal area faint, posterior one distinct. Lunule long, narrow, oval, shallow, composed of a projection in right valve fitting into a recess in left. Ligament external. Anterior adductor scar of normal length and width, generally curved, diverging from pallial line. Anterior pedal retractor scar separate from adductor, posterior one not evident. Anterior and posterior laterals single in right valve, double in left; two cardinals, about equally strong, in each valve; right posterior cardinal not bifid. Pallial blood vessel scar present. Inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — The only Western Hemisphere species unequivocally assignable to *Epilucina* is the type species. It is commonly found living from northern California to Baja California. Grant and Gale (1931) gave its stratigraphic range as late Pliocene to Recent; all the fossil occurrences which they cite for *E. californica* are in southern California or Baja California.

B. L. Clark (1946) described *Lucina (Epilucina) gabrielensis* from late Eocene rocks of Colombia. He stated that this species resembled *Miltha* in size and shape, but that the presence of lateral teeth indicated placement in *Epilucina.* Only a left valve was found, and, as I have not seen the specimen and the hinge was not figured, its assignment to *Epilucina* cannot be confirmed or denied here.

*E. californica* seems to have its closest affinities with either *Myrtea* or *Codakia.* The resemblance between *M. (M.) spinifera* and the more elongate individuals of *E. californica* is particularly striking (cf. Pl. 34, fig. 9, and Pl. 35, fig. 2). These species are similar in shape, in having only concentric sculpture, in having well-developed anterior and posterior laterals, and in having an external ligament. The geographical distribution of *E. californica,* which ranges farther north than most other West Coast lucinids, may indicate physiological similarity to the cold-water *Myrtea* lineage. *E. californica* attains a somewhat larger adult size than do species of *Myrtea;* also, it has only one order of concentric ribs, lacks posterodorsal spines, has a much more strongly asymmetrical lunule, a differently shaped anterior adductor scar, two cardinal teeth in the right valve rather than one, lacks a posterior pedal retractor scar, and has a pallial blood vessel scar. The musculature, dentition, and lunule of *E. californica* recall *Codakia s. s.,* from which it differs in lacking radial sculpture and in having an external ligament and well-developed posterior laterals. In *E. californica* the ligament and dentition are similar to those of *Codakia (Ctena).* The species shares with both subgenera of *Codakia* the smooth posterodorsal margin and the presence of the pallial blood vessel scar.

These features may indicate that Chavan's placement of *Epilucina* in *Codakia* was correct, but two species may link *Epilucina* and *Myrtea.* One, *Lucina roseburgensis* Hendon (*in* Turner, 1938), was made the type species of *Myrtucina* Vokes, 1939, proposed as a subgenus of *Myrtea.* This Eocene species from Oregon unfortunately could not be included in the phenetic study because available specimens were too poorly preserved to yield sufficient characters. *Myrtucina roseburgensis* is similar in shape to *Epilucina californica,* though it is larger, attaining a length of 42 mm (Turner, 1938; Vokes, 1939). The posterior end of the shell in *Myrtucina roseburgensis* is strongly truncated, almost straight; a similar truncation exists in some individuals of *E. californica* (Pl. 35, fig. 1). The lunule and surface sculpture of *M. roseburgensis* are like those of *E. californica,* but the dentition is like that of *Myrtea spinifera,* since there is only one cardinal in the right valve. The musculature of *M. roseburgensis* is unknown.

*Lucina occidentalis* Morton, 1842, from the Late Cretaceous (Maestrichtian) of the Western Interior, is the type species of *Nymphalucina* Speden, 1970. Speden's specimens in the Yale Peabody Museum collections are reminiscent of *Myrtucina roseburgensis*. They are of about the same size and shape, and some individuals of *Nymphalucina occidentalis* show posterior truncation. In some but not all individuals of *N. occidentalis,* the surface sculpture is differentiated into first-order and second-order concentrics. The dentition is like that of *Epilucina,* and the pallial blood vessel scar is well marked. The lunule is shaped like that of *Epilucina* but is nearly symmetrical. The anterior adductor scar, straight and diverging from the pallial line, and the presence of both pedal retractor scars recall *Myrtea s. s.* Small specimens have posterodorsal spines.

Speden compared *Nymphalucina* to Chavan's genera *Jagolucina* (Chavan, 1937), first considered closely related to *Ctena* but later placed near *Miltha s. s.*, and *Jagonoma* (Chavan, 1946b), believed ancestral to *Ctena. Jagonoma* originated in Jurassic time; *Jagolucina* was originally considered to be of equal antiquity but was later restricted to Paleocene and Eocene species (Chavan, 1946b). Speden also stated that *Lucina linearia* Stephenson, 1941, whose probable placement in *Myrtea s. s.* has been discussed above, might belong to *Nymphalucina.* He also included as probably congeneric with *N. occidentalis* another small species, *Lucina dentonana* Stephenson, 1952, from the Upper Cretaceous (Cenomanian) Woodbine Formation of Texas.

### **Myrtea? (Epilucina) californica** (Conrad)

Plate 35, figures 1-3

*Lucina californica* Conrad, 1837, p. 255, pl. 20, fig. 1.
*Phacoides (Epilucina) californica* (Conrad), Dall, 1901b, pp. 806, 813; Dall, 1903, p. 1381; Lamy, 1920, p. 188; Thiele, 1935, p. 866.
*Lucina (Myrtea) californica* Conrad, Grant and Gale, 1931, pp. 285-286, pl. 14, figs. 15a, 15b, 21a, 21b.
*Codokia (Epilucina) californica* (Conrad), Chavan, 1937, pp. 272, 274, 277, [not] fig. 10.
*Codakia (Epilucina) californica* (Conrad), Abbott, 1954, pp. 390-391, pl. 31c; Chavan, 1969, p. *N*494, [not] fig. E3, 13a, 13b.
? *Lucina artemidis* Carpenter, 1857, p. 201; Palmer, 1963, p. 304.

*Description.* — Shell of medium size (median length of 18 specimens 27 mm, range 12-38 mm), slightly to distinctly longer than high (median H/L 0.93, range 0.86-0.97), moderately inflated (median D/L 0.27, range 0.22-0.31), anterior expansion generally moderate (median A/L 0.48, range 0.44-0.55). Shape of posterior margin sometimes rounded (Pl. 35, fig. 2), sometimes truncate (Pl. 35, fig. 1). All other characters as in generic diagnosis.

*Types.* — Keen (1966) was unable to locate the type of *Lucina californica* in the Nuttall Collection of the British Museum (Natural History), in which a number of West American species described by Conrad are housed.

*Material.* — The phenetic study was based on about 20 Recent specimens, all from central and southern California, in the collections of the Yale Peabody Museum and the National Museum of Natural History.

*Discussion.* — The geographic range of living representatives of *Myrtea? (Epilucina) californica* is given by Grant and Gale (1931) as from Crescent City, California, (just south of the Oregon-California state line) to San Ignacio Lagoon, at about the midpoint of the west coast of Baja California. This species thus ranges farther to the north, but less far to the south, than most other West Coast lucinids. It is commonly found in southern California in the intertidal zone, particularly on exposed rocky shores (Abbott, 1954; Valentine, 1961).

Although Conrad's (1837) figure of *Lucina californica* is not good, and his original specimens have not been found, I believe it unlikely that Chavan's (1937, 1969) figures represent a form which is conspecific with Conrad's *L. californica.*

Dall (1901b) considered *Lucina artemidis* Carpenter, collected at Acapulco, Guerrero, Mexico, to be the young of *M.? (E.) californica.* If so, the southward range of *californica* would be considerably extended. Unfortunately, the type of *artemidis* has apparently been lost (Palmer, 1963).

## Genus **ANODONTIA**

### Subgenus **ANODONTIA**

*Pegophysema* Stewart, 1930, p. 38, 185.
*Prophetilora* Iredale, 1930a, p. 75.
*Lissosphaira* Olsson, 1961, p. 221.

*Author.* — Link, 1807, p. 156.

*Type species.* — *Anodontia alba* Link, 1807, p. 156 (= *Venus edentula* Gmelin, 1791, p. 3286, ? *non V. edentula* Linné, 1758, p. 689), by monotypy.

*Discussion.* — There has been controversy over the identity of *Anodontia alba* Link. Link (1807), who introduced the name *Anodontia,* described the genus as being without teeth. He proposed a new name, *A. alba,* and cited *Venus edentula,* apparently as a synonym of it, referring to Gmelin (1791, p. 3286) and to Chemnitz (1784, pl. 39, figs. 410, 411). The cited figures in Chemnitz, however, actually illustrate a venerid. Figures 408 and 409 on the same plate, just above the numerals "410" and "411", represent *Venus jamaicensis* Chemnitz (= *Tellina pectinata* Gmelin). The species which Chemnitz called *Venus edentula* is illustrated on his plate 40, figures 427 to 429. Stewart (1930) believed that Link had intended to cite the figures of *Venus jamaicen-*

*sis* as illustrating *Anodontia alba.* He thus considered *Phacoides* a junior synonym of *Anodontia.* He surmised that in speaking of *Anodontia* as being without teeth Link had alluded only to the obsolescent cardinals of *V. jamaicensis.*

Chavan (1937) rejected Stewart's explanation, but offered no alternative, and used the name *Anodontia* for some of the edentulous lucinids. Later, however, Gardner (January, 1951) and Eames (June, 1951) independently proposed a convincing explanation of the discrepancy between Link's description and his figure citation. In his description of *Venus edentula,* Gmelin (1791) referred to plate 40, figures 427 to 429, of Chemnitz. On the same page, just above the description of *V. edentula,* he described *Venus scripta,* citing plate 39, figures 410 and 411, of Chemnitz. Gardner and Eames both suggested that Link had taken the reference to Chemnitz directly from Gmelin and had erroneously copied the reference to *V. scripta.*

According to Lamy (1920), *Venus edentula* Linné is an Indo-Pacific species, whereas the species figured by Chemnitz and called *V. edentula* by Gmelin and *Anodontia alba* by Link is found in southeastern North America and the Caribbean. One of the principal distinguishing features, according to Lamy, is the orange color of the shell interior in the Western Hemisphere species. Dodge (1952) considered it possible that Linné's specimen of *Venus edentula* might simply have been one which was so faded that the internal color was not noticeable enough to be mentioned in the description. Linné gave the locality of *V. edentula* as "in Indiis", a phrase which, Dodge pointed out, could refer to the West Indies. Dodge was unable to locate the specimen described by Linné. Though he believed that the identity of *V. edentula* Linné with the West Indian shell was fairly certain, he recognized that using the name *A. alba* for this species, as I shall do here, was perhaps the more conservative course.

Chavan (1938, 1969) considered *A. alba* synonymous with *V. edentula* Linné but apparently believed both to be Indo-Pacific species (Link did not specify a locality for *A. alba*). Chavan differentiated *Anodontia* from *Pegophysema* Stewart, 1930, to which he referred the Caribbean taxon which I have here called *A. alba,* saying that the ligament of the Indo-Pacific species is deeply inset rather than external. I believe that he is mistaken about the identity of *Anodontia alba.*

As noted in the discussion of *Lucina,* many early workers — Fischer (1887), Dall (1901b), Lamy (1920), Thiele (1935) — used the name *Lucina* to refer to the edentulous lucinids, considering *V. edentula* the type of *Lucina.*

*Diagnosis.* — Shell of large to very large size, thin, longer than high, strongly inflated, anterior expansion small or moderate. Surface sculpture concentric, fine to distinct, with irregularly spaced growth rings; dorsal areas faint to distinct. Lunule long, shallow, variable in shape. Ligament external or slightly inset. Anterior adductor scar of normal length and width, variable in shape and position; posterior adductor scar elliptical. Anterior pedal retractor scar separate from adductor, posterior one not evident. Hinge plate narrow; hinge edentulous. Pallial blood vessel scar present; inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — According to the compilation by Lamy (1920), *Anodontia* has a world-wide distribution, in tropical and subtropical waters, in the Recent fauna. There are four North American species: *Anodontia (Anodontia) alba* Link, 1807; *A. (A.) philippiana* (Reeve, 1850); *A. (A.) phenax* (Dall and Simpson, 1901); and *A. (A.) edentuloides* (Verrill, 1870). The first three are from eastern North America and the Caribbean, and the fourth from western Mexico. Stewart (1930) made *A. (A.) philippiana* the type species of *Pegophysema;* the status of that name is discussed under that species. Iredale (1930a) introduced the name *Prophetilora* for an Australian species, *P. arizela* Iredale, 1930a, which seems to closely resemble *A. alba.*

Mansfield (1932) reported *A. (A.) alba* from the upper Miocene (Choctawhatchee Formation), the Pliocene (Caloosahatchee Formation), and the Pleistocene of Florida (Mansfield, 1932). Olsson (1961) designated *Lucina spherica* Dall and Ochsner, 1928, a Pliocene species from the Galapagos Islands, as the type species of *Lissosphaira,* a subgenus of *Anodontia.* This name seems unnecessary, because the subgenus is distinguished only by having better-marked dorsal areas than *Anodontia s. s.* Grant and Gale (1931) reported *A. (A.) edentuloides* (Verrill, 1870) from the Pliocene of Southern California.

Dall (1903) described three species of *Anodontia* — *janus, corpulenta,* and *santarosana* — from the middle Miocene Alum Bluff Group of Florida. The shell of the third species shows alternate light and dark bands, which may be analogous to the color banding seen on some Recent individuals of *A. (A.) alba.* A contemporaneous species is *A. (A.) bowdenensis* (Woodring, 1925), from the Bowden Formation of Jamaica.

An unnamed lucinid which may belong to *Anodontia s. s.* is found associated with *Miltha (Lucinoma) acutilineata* Conrad in the middle Miocene Astoria Formation of Washington (R. E. Young, personal communication). In size and inflation this species closely resembles *A. (A.) alba;* the hinge is not known. One internal mold shows a straight anterior adductor scar which, like that of *A. (A.) philippiana,* diverges sharply from the pallial line. This is the earliest known West Coast species of *Anodontia s. s.* and the only species of the subgenus found associated with a cold-water fauna.

Three South American species belonging to *Anodontia s. s.* are *A. (A.) stainforthi* Marks, 1951, and *A. (A.) thalmanni* (Marks, 1951), both from the middle Miocene of Ecuador; and *A. (A.) sechura* (Olsson, 1932), from the early Miocene of Peru. The two latter species were originally placed in *Pegophysema* Stewart. Musculature and other internal features of all these species are unknown. There are two Oligocene representatives of the subgenus—*A. (A.) perlevis* (Conrad, 1848), from the middle Oligocene Vicksburg Group of Mississippi, and *A. (A.) inca* (Olsson, 1930b), from the early Oligocene Chira Formation of Peru.

Stewart (1930) proposed the name *Eophysema* for small Eocene species with cardinal teeth; he believed these to be ancestral to the edentulous species of *Anodontia s. s.* There is a large middle Eocene species, *Anodontia? augustana* Gardner, 1951, from the Tallahatta Formation of Alabama, whose size (length about 88 mm) and strong inflation make it seem probably consubgeneric with *A. (Anodontia) alba.* It is preserved only as internal molds, some with attached fragments of shell material, and clearly shows an elongate anterior adductor scar. The dention is not preserved on any of the specimens I have seen.

*Lucina corbula* Olsson, 1929, from the Eocene Restin Formation of Peru, probably belongs to *Anodontia s. s.* or *Eophysema,* but no internal features are known. No Mesozoic species which could be referred to *Anodontia s. s.* or *Eophysema* were reported by Chavan (1938), nor have I seen any such species. The relationship between *Anodontia s. s.* and *Eophysema* and their probable kinship to other lucinid lineages are discussed under *Eophysema.*

### **Anodontia (Anodontia) alba** Link

Plate 35, figures 4-6

*Venus edentula* Gmelin, 1791, p. 3286 [*?non Venus edentula* Linné, 1758, p. 689].
Not *Anodontia edentula* (Linné), Chavan, 1938, pp. 121-122.
*Loripinus (Pegophysema) edentula* (Linné), Stewart, 1930, p. 186.
*Anodontia alba* Link, 1807, p. 156; Abbott, 1954, p. 389, pl. 38f; Warmke and Abbott, 1961, pp. 177-178, pl. 36e.
*Tellina chrysostoma* Meuschen, 1787, p. 482 [non-binomial].
*Lucina chrysostoma* Philippi, 1845, p. 181; Dall, 1901b, p. 802; Dall, 1903, pp. 1354-1355; Lamy, 1920, pp. 86-88; Mansfield, 1932, p. 95, pl. 19, figs. 2, 3.
*Cavilucina (Pegophysema) chrysostoma* (Philippi), Chavan, 1938, p. 120.
*Loripinus (Pegophysema) chrysostoma* (Philippi), DuBar, 1958, pp. 166-167.
*Pegophysema (Pegophysema) chrysostoma* (Meuschen), Chavan, 1969, p. *N*504, fig. E9, 12.

*Description* — Shell thin, of large size (median length of 21 specimens 47 mm, range 36-57 mm), longer than high (median H/L 0.91, range 0.88-0.97), strongly inflated (median D/L 0.32, range 0.25-0.42), anterior expansion usually small (median A/L 0.41, range 0.34-0.51). Sculpture concentric, fine; growth rings irregularly spaced. Some specimens have one or more concentric bands, about 5 mm wide and purple in color, on shell exterior. Anterior dorsal area distinct, posterior one faint. Lunule long, narrow, shallow, generally rectangular, asymmetrical (wider part on right valve). Ligament external or slightly inset. Anterior adductor scar of normal length and width, straight, parallel to pallial line; posterior adductor scar elliptical; anterior pedal retractor scar separate from adductor, posterior one not evident. Hinge plate narrow; hinge edentulous. Shell interior orange; color deepest in region of pallial line and muscle scars. Pallial blood vessel scar present. Inner ventral margin smooth.

*Types.* — Dance (1966) stated that Link's specimens are in the Rostock Museum, but that his specimens were not isolated from other collections and none can now be positively identified. Dodge (1952) was unable to locate Linné's specimen of *V. edentula* in the Linnean Society of London's collection. In the collection of Queen Louisa Ulrica of Sweden, for which Linné (1764) prepared a descriptive catalogue (this collection is now housed in the Zoology Institute of the University of Uppsala), there is a specimen identified as *V. edentula.* Dodge believed that this might be the one on which Linné's description was based, but he stated that because the labels on the "Museum Ulricae" specimens are not in Linné's handwriting, these specimens cannot be unequivocally identified as his types.

*Material.* — The phenetic study was based on about 35 specimens in the Yale Peabody Museum collections. Recent specimens examined were from Florida, South Carolina, Texas, and Jamaica; Pleistocene and Pliocene ones were from Florida.

*Discussion.* — Apparently two different species, one Indo-Pacific and one North American, have been called *Venus edentula* (see discussion above of the type species of *Anodontia*). The name *Tellina chrysostoma* Meuschen, 1787, frequently used for the North American species, is from a shell catalogue ("Museum Geversianum"), in which the nomenclature was not consistently binomial (Stewart, 1930; Dance, 1966). Chavan (1937, 1938) identified *Anodontia alba* Link with Linné's *Venus edentula* rather than with *"Tellina chrysostoma"*, and considered *A. alba* to be generically distinct from that species and the species here called *A. (A.) philippiana* (Reeve). The distinction was based on the inset ligament and traces of a cardinal tooth seen in the Indo-Pacific species. Monterosato (1883) established the genus *Loripinus* for a Mediterranean species, *Lucina fragilis* Philippi, 1836. According to Dall (1901b), this species has an internal ligament and a short, wide anterior adductor scar. Chavan (1938) formerly synonymized *Loripinus* with *Anodontia*, but he later treated it as a subgenus of *Anodontia* (Chavan, 1969). From Dall's description, *Loripinus fragilis* appears to be more similar to species here included in *Loripes* than to those which I assign to *Anodontia*.

According to Stanley (1970), in Florida *A. (Anodontia) alba* inhabits intertidal, often grassy environments. In the upper part of the intertidal zone it occurs with *Lucina (Phacoides) pectinata*, and in the lower part it is found with *Codakia (Codakia) orbicularis*. It lives buried more deeply than either of these species, both of which are of roughly the same size as *A. (A.) alba*, but more compressed. Stanley considered that strongly inflated species such as *A. (A.) alba* tend to be sluggish burrowers; deep burial is thus advantageous for them because they are not likely to be disinterred under normal conditions. The possession of thin shells with little surface ornamentation is also characteristic of deep burrowers, which by their position in the substratum do not need protection against mechanical abrasion or predation, or strong ornamentation for stabilization (Stanley, 1970).

### **Anodontia (Anodontia) philippiana** (Reeve)

Plate 35, figures 7-10

*Lucina edentula* Philippi, 1847, pl. 1, fig. 1 [*non Venus edentula* Linné, 1758, *nec Venus edentula* Gmelin, 1791].
*Lucina philippiana* Reeve, 1850, pl. 5, fig. 23a, b; Dall, 1901b, p. 802; Dall, 1903, p. 1355.
*Lucina edentula* var. *philippiana* Reeve, Lamy, 1920, p. 80.
*Anodontia philippiana* (Reeve), Chavan, 1938, p. 124; Abbott, 1954, pp. 389-390, pl. 38e; Warmke and Abbott, 1961, p. 178.
*Lucina schrammi* Crosse, 1876, p. 166; Crosse, 1878, p. 328, pl. 20, fig. 6; Lamy, 1920, p. 85.
*Loripinus (Pegophysema) schrammi* (Crosse), Stewart, 1930, pp. 185-186; Olsson and Harbison, 1953, pp. 80-81; DuBar, 1958, p. 167.
*Cavilucina (Pegophysema) schrammi* (Crosse), Chavan, 1938, pp. 119, 120.
*Pegophysema (Pegophysema) schrammi* (Crosse), Chavan, 1969, p. *N*504.

*Description.* — Shell thin, of large to very large size (median length of 19 specimens 66 mm, range 50-105 mm), longer than high (median H/L 0.90, range 0.85-0.96), strongly inflated (median D/L 0.34, range 0.25-0.41), anterior expansion small (median A/L 0.40, range 0.25-0.46). Surface sculpture fine, concentric; growth rings irregularly spaced; dorsal areas faint. Periostracum thin, brown, patchy. Shell white, no internal or external color. Lunule long, wide, rectangular, shallow, symmetrical or only slightly asymmetrical. Ligament external or only slightly inset. Anterior adductor scar of normal length and width, ventral two-thirds bent strongly away from dorsal portion and from pallial line; posterior adductor scar elongate. Pedal musculature, hinge, and other internal features as in *A. (A.) alba*, except for absence of color.

*Types.* — I have not seen the type specimens of either *Lucina philippiana* Reeve or *Lucina schrammi* Crosse. Crosse's collection is in the Muséum national d'Histoire naturelle, Paris. Reeve's specimens of *L. philippiana* were in th collection of Hugh Cuming, which is now in the British Museum (Natural History) (Dance, 1966).

*Material.* — The phenetic study was based on about 20 Recent specimens, from Florida, Texas, Bermuda, and the Caribbean, in the collections of the Yale Peabody Museum.

*Discussion.* — In synonymizing *Lucina philippiana* Reeve, 1850, and *Lucina schrammi* Crosse, 1876, I am following Dall (1901b), who considered them the same species. Reeve (1850) stated that the specimen figured by Philippi (1847) differed from Linné's *V. edentula* in being more opaque and in having a thin periostracum. Reeve apparently did not know the habitat of *L. philippiana*. Crosse (1876) gave the type locality of *L. schrammi*, which he stated to be more strongly inflated than *L. philippiana*, as Guadeloupe, in the West Indies. Lamy (1920) and Chavan (1938) believed *L. philippiana* Reeve to be from the Indo-Pacific. Both authors considered that there were two closely related Indo-Pacific species—*Lucina philippiana* Reeve and *L. edentula* (Linné) — and two closely related Caribbean species — *Lucina chrysostoma* Philippi (= *Venus edentula* of Gmelin) and *L. schrammi* Crosse. Lamy believed *L. chrysostoma* to be synonymous with *Anodontia alba* Link, but Chavan thought that *L. edentula* (Linné) and *A. alba* were the same species. Accordingly, Chavan placed *L. philippiana* and *L. edentula* in *Anodontia*, and *L. chrysostoma* and *L. schrammi* in *Pegophysema*.

Stewart (1930), as noted above, used *Anodontia* for the group of species here placed in *Phacoides*. He, therefore, proposed the name *Pegophysema*, as a subgenus of *Loripinus* Monterosato, 1883, for the large, strongly inflated, edentulous lucinids with an elongated anterior adductor scar; he designated *L. schrammi* Crosse as type species. Stewart noted that the West Indian species here identified as *Ano-*

*dontia alba* was closely related to and perhaps conspecific with *L. schrammi.* In essence, then, his name *Pegophysema* was simply a replacement name for *Anodontia.*

Olsson and Harbison (1953) believed *A. (A.) alba* and *A. (A.) philippiana* to be conspecific, stating that the greater divergence of the anterior adductor scar from the pallial line in the larger species might be a consequence of ontogenetic change, the position of the anterior adductor changing as the shell increased in size and became more inflated. Comparison of shells of the same size representing the two species (Pl. 35, figures 5, 7) shows, however, that the position of the anterior adductor is the same for both small and large individuals of *A. (A.) philippiana.* Several other differences — the presence of internal color in *A. (A.) alba* and of a periostracum in *A. (A.) philippiana,* differently shaped lunules — indicate that there are indeed two species, with *A. (A.) philippiana* attaining a larger average adult size than *A. (A.) alba.*

### Subgenus **EOPHYSEMA**

*Author.* — Stewart, 1930, p. 37, 186.

*Type species.* — *Lucina subvexa* Conrad, 1833c, p. 40, by original designation.

*Discussion.* — Stewart (1930) proposed *Eophysema* as a subgenus of *Loripinus.*

*Diagnosis.* — Shell thin, of very small to medium size, longer than high, moderately inflated. Surface sculpture dominantly concentric, with fine radials. Dorsal areas faint to distinct. Lunule long, wide, triangular, shallow. Ligament external. Anterior adductor scar narrow, of normal length, bent away from pallial line; posterior adductor scar round. Anterior pedal retractor scar separate from adductor, posterior one not evident. Hinge plate narrow; hinge edentulous or with obsolescent anterior and posterior laterals, and with one cardinal in right valve and two in left. Pallial blood vessel scar present. Inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — Stewart (1930) included in *Eophysema* the middle Eocene type species, *L. subvexa* Conrad; an early Eocene species, *L. ozarkana* Harris, 1897 (both from Alabama); and a middle Eocene species from the Paris Basin, *L. menardi* Cossmann and Pissarro, 1906. He noted that one Oligocene species, *Lucina perlevis* Conrad, 1848, and one from the middle Miocene, *L. janus* Dall, 1903, resembled *Eophysema subvexa* in configuration and in the presence of radial sculpture. Because both are edentulous, however, he assigned them to *Pegophysema (= Anodontia s. s.),* believing that they might be transitional between *Eophysema* and *Pegophysema.*

Chavan (1938) considered *Lucina menardi* to belong to *Pegophysema (= Anodontia s. s.);* and, as stated in the discussion of the subgenus *Myrtea s. s.,* he included *L. ozarkana* in *Gardnerella,* which he proposed as a subgenus of *Myrtea* (Chavan, 1951b). Because the definition and relationships of the subgenus *Eophysema* are contingent upon an understanding of the taxonomic problems involving its type species, discussion of the phylogenetic position of *Eophysema* is deferred to the section on *A. (E.) subvexa.*

### **Anodontia (Eophysema) subvexa** (Conrad)

Plate 35, figures 11-13

*Lucina subvexa* Conrad, 1833c, p. 40; Conrad, 1846, p. 403, pl. 4, fig. 14; Dall, 1903, p. 1352-1353.
*Lucina (Loripes) subvexa* Conrad, Harris, 1919, pp. 119-121, pl. 39, figs. 1, [?]4, [not]2.
*Loripinus (Eophysema) subvexa* (Conrad), Stewart, 1930, pp. 37, 186.
*Anodontia subvexa* (Conrad), Chavan, 1938, p. 123.
*Eophysema subvexa* (Conrad), Palmer and Brann, 1965, pp. 139-140.
*Lucina (Loripes) subvexa* var. *sylvaerupis* Harris, 1919, p. 120, pl. 39, figs. 3, 5, 5a.
"*Lucina*" *sylvaerupis* Harris, Palmer and Brann, 1965, p. 184.
Not *Lucina (Loripes) subvexa* Harris, 1919, p. 120, pl. 39, fig. 2.
*Pegophysema (Eophysema) subvexa* (Conrad), Chavan, 1969, p. *N*504.

*Description.* — Shell thin, of very small to medium size (median length of 11 specimens 12 mm, range 5-32 mm), longer than high (median H/L of 11 specimens 0.90, range 0.83-0.96), moderately inflated (median D/L of 5 specimens 0.26, range 0.24-0.30), anterior expansion moderate to great (median A/L of 11 specimens 0.50, range 0.33-0.53). Sculpture dominantly concentric, often with fine, continuous radials; no growth rings. Dorsal areas distinct on small specimens, faint on larger ones. Lunule long, wide, triangular, shallow. Ligament external. Anterior adductor scar narrow, of normal length, slightly bent, and diverging from pallial line; posterior adductor scar round. Anterior pedal retractor scar separate from adductor, posterior one not evident. Hinge plate narrow; small specimens have one cardinal in right valve, two in left, and traces of laterals (Pl. 35, fig. 12); larger specimens edentulous. Inner ventral margin smooth; pallial blood vessel scar present.

*Types.* — A broken left valve in the Academy of Natural Sciences of Philadelphia (ANSP 30501) was figured by Harris (1946), and E. J. Moore (1962) cited it as the "probable holotype" of *Lucina subvexa.* Stewart (1930, p. 186) stated that "Conrad's types are in the [Philadelphia] Academy; only the immature specimen (length 11 mm) has the hinge preserved". Apparently the smaller specimen to which Stewart referred has been lost.

*Material.* — The phenetic study was based on 11 specimens of early and middle Eocene age from Alabama and Mississippi, in the collections of the National Museum of

Natural History. The type specimen at the Philadelphia Academy, and the specimens figured by Harris and housed in the Paleontological Research Institution (PRI 760-762) were subsequently examined.

*Discussion.* — Conrad (1833c) described *Lucina subvexa* as being edentulous. He did not indicate the size of the species, but the type specimen is about 25 mm long. Conrad stated that the species came from what is now called the Gosport Sand at Claiborne, Alabama, but later workers found it only in the underlying Lisbon Formation (Stewart, 1930; Harris, 1946). Dall (1903) suggested that small middle Eocene specimens, less than 10 mm in length and with small cardinals and traces of laterals, were juveniles of *L. subvexa.* Harris (1919) included in *L. subvexa* three groups of species: medium-sized, edentulous forms; smaller specimens with distinct teeth, to which he gave the varietal name *sylvaerupis;* and large individuals, attaining a size of 76 mm. Most of the specimens which Harris described came from the middle Eocene "St. Maurice Group" (Lisbon Formation) of Alabama, but the type species of *sylvaerupis* was from the "Sabine Group" [Hatchetigbee Formation, Wilcox Group, early Eocene (Palmer and Brann, 1965)] in Alabama.

Stewart (1930), following Dall, considered *L. subvexa* var. *sylvaerupis* and *L. subvexa s. s.* to be successive growth stages of a single species, in which the cardinal dentition was effaced during ontogeny in a manner analogous to the reduction of the cardinals in *Phacoides.* In his proposal of the subgenus *Eophysema,* Stewart specified that this group was one in which "the immature specimens, at least" had cardinal teeth.

Gardner (1951) proposed the name *Anodontia*? *augustana* for large middle Eocene individuals whose dentition is unknown. Palmer and Brann (1965) synonymized Harris's (1919) large specimens called *L. subvexa* with *A.*? *augustana* Gardner, gave separate specific status to the specimens to which he had given the varietal name *sylvaerupis,* and restricted the name *Eophysema subvexa* to the edentulous forms of medium size. They considered it probable that the large specimens synonymized with *A.*? *augustana* had come from the middle Eocene Tallahatta Formation which underlies the Lisbon Formation.

In the phenetic study I included both specimens which Palmer and Brann would place in *"Lucina" sylvaerupis* (Pl. 35, fig. 12, 13) and specimens corresponding to *Eophysema subvexa* in the restricted sense (Pl. 35, fig. 11). I, therefore, followed Stewart's concept of the subgenus *Eophysema.* It is difficult to determine whether or not two species were actually represented in the available material, especially because nearly all the larger individuals were preserved as internal molds or articulated specimens, showing no dentition. A group of six specimens in the study ranged from 5 to 12 mm in length; the other five, from 19 to 32 mm. All of the latter group, however, were from a single locality (Claiborne, Alabama), whereas the former were from several different localities in western Alabama and eastern Mississippi. In addition, stratigraphic data for most of the specimens was given only in such general terms as "Sabine" (early Eocene) and "St. Maurice" (middle Eocene, excepting the Gosport Sand); locality data were too vague to permit more exact determination of the horizon from which the specimens were probably collected.

The name *Lucina ozarkana* Harris, 1897, was proposed for early Eocene species of about the same size as *Eophysema subvexa* "var. *sylvaerupis*", with more pronounced radial sculpture which is usually discontinuous, like that of *Myrtea (Eulopia).* Harris (1919, 1946) also used the name *L. ozarkana* to refer to middle Eocene specimens about 30 to 50 mm long, and to late Eocene specimens comparable in size to the early Eocene ones. *L. ozarkana* has small cardinal teeth. As previously noted, Chavan (1951b) included *L. ozarkana* in his subgenus *Myrtea (Gardnerella),* which is also defined as having small cardinals. If Palmer and Brann's restriction of the name *Eophysema subvexa* to the edentulous middle Eocene specimens proves to be justifiable on the ground that the dentate and edentulous forms actually belong to different species, *Eophysema* may have to be synonymized with *Anodontia s. s.* and the name *Gardnerella* used for dentate, strongly inflated Eocene to Miocene species of small to medium size. I believe, however, that the dentate and edentulous forms included under *E. subvexa* are at least consubgeneric if not conspecific. I thus have retained the name *Eophysema* in the sense in which Stewart used it.

Of the several lucinid lineages recognized in this study, the *Anodontia* lineage is the only one which seems to be exclusively Cenozoic. The similarity in sculpture and outline of some of its species to species of the *Myrtea* lineage, and the inclusion in *Gardnerella* of some species previously placed in *Myrtea* and others originally assigned to *Eophysema,* may indicate a close relationship between the *Myrtea* and *Anodontia* lineages. Chavan (1938) formerly believed the *Anodontia* lineage to be derived from *Monitilora* Iredale, 1930b, a Paleocene to Recent group whose fossil record is principally European and which has living representatives in Australia. [He originally placed *Myrtea (Gardnerella) waltonensis* in *Montilora.*] He traced *Monitilora* to the Jurassic and Cretaceous *Mesomiltha,* which he also considered ancestral to *Miltha* and *Myrtea.* He later placed *Anodontia* and *Eophysema* in the subfamily Milthinae and *Gardnerella* and *Monitilora* in the Myrteinae (Chavan, 1969). I consider these four taxa to be considerably more similar than Chavan's taxonomic treatment of them indicates.

### Genus **LORIPES**

### Subgenus **LORIPES**

*Loripoderma* Poli, 1795, p. 253.
*Lucinida* d'Orbigny, 1846, p. 588.

*Author.* — Poli, 1791, p. 31.

*Type species.* — *Loripes lacteus* Poli, 1791, p. 31; Poli, 1795, p. 46, pl. 15, figs. 28-29, by monotypy.

*Discussion.* — Some authors, such as Stewart (1930), challenged Poli's generic names because he used a dual system of names — one name for the animal inhabiting the shell and another for the shell itself. The names for the "animals" were proposed in the first volume of Poli's work; in the second part, the "shell" names were created by adding the suffix *"derma"* to the "animal" names. For example, *Loripes* Poli, 1791, became *Loripoderma* Poli, 1795. He used both sets of names with Linnean specific names; thus his nomenclature was clearly binomial. It is thus permissible to accept his "animal" names proposed in 1791, treating the "shell" names of 1795 as their junior objective synonyms. This action is consistent with the International Code of Zoological Nomenclature, which states [Art. 24(b)] that the law of priority applies "when any part of an animal is named before the whole animal".

*Diagnosis.* — Shell small, slightly longer than high, moderately inflated, anterior expansion moderate to great. Surface sculpture concentric, fine; growth rings irregularly spaced; dorsal areas fine to distinct. Lunule long, wide, triangular, slightly asymmetrical, shallow. Ligament long, completely internal, set in a groove diagonal to the dorsal margin. Anterior adductor scar of normal length and width, bent away from pallial line; posterior adductor scar elliptical. Anterior pedal retractor scar separate and posterior one partly separate from adductors. Laterals absent or obsolescent; when present, single in right valve and double in left. One cardinal in right valve, two in left. Pallial blood vessel scar present; inner ventral margin smooth.

*Distribution and phylogenetic relationships.* — The type species of *Loripes* is common in European seas (Lamy, 1920). Chavan (1937) listed three other Recent species of *Loripes s. s.,* from the Mediterranean, Madagascar, and Brazil. He also recognized three subgenera of *Loripes,* in addition to the typical subgenus. Two of these, *Wallucina* Iredale, 1930b, and *Pillucina* Pilsbry, 1921, have Recent representatives. Both are found in Australia, Japan, and the Indian Ocean; *Pillucina* also occurs in Hawaii. Except for the Brazilian *Lucinida cryptella* d'Orbigny, 1846 [Chavan (1937) synonymized *Lucinida* d'Orbigny, 1846, with *Loripes*], and a species from British Honduras, *Lucina clausa* Philippi, 1849, which Dall (1901b) provisionally assigned to *Loripes,* the group is not represented in the Western Hemisphere. Though the name *Loripes* has sometimes been used for species here placed in the *Anodontia* lineage, no true fossil representatives of *Loripes* have been reported from North America or South America.

Chavan (1937) traced the history of *Loripes s. s.* in Europe from early Miocene time to the present. The subgenus *Wallucina* is reported from the Japanese Miocene (Chavan, 1938). Another subgenus, *Microloripes,* was reported by Chavan (1937) to have existed from Paleocene to Miocene time in Europe, with one possible Recent representative in Mauritania, and to be the probable ancestor of the other subgenera of *Loripes.* Chavan then considered *Loripes* to have its closest affinities with *Ctena,* believing *Ctena, Loripes,* and *Codakia* to be related but giving all separate generic status. The internalization of the ligament in *Loripes* was considered homologous with that in *Codakia.* Chavan (1937) first traced *Loripes* to *Jagolucina,* proposed as a Jurassic to Eocene subgenus of *Ctena* whose earlier members were believed ancestral to *Ctena.* In his subsequent restriction (Chavan, 1946b) of *Jagolucina* to a few Paleocene and Eocene species believed more closely related to *Saxolucina* and *Miltha,* and establishment of a new subgenus *Jagonoma* for the probable ancestors of *Ctena,* Chavan did not mention the possible affinities of *Loripes.*

Chavan *in* 1969 placed *Loripes, Microloripes, Wallucina, Pillucina,* and *Sydlorina* Iredale, 1930b [formerly synonymized with *Pillucina* (Chavan, 1938)], as well as *Codakia* and related taxa, in the subfamily Lucininae. He treated *Microloripes* as a subgenus of *Parvilucina,* a concept suggested by Cossmann and Peyrot (1911), who noted that *Lucina dentata* Defrance, 1823, the Miocene type species of *Microloripes,* resembles species of *Parvilucina* except for the internal ligament. In its very small size, rounded shape, concentric sculpture, and dentition (two cardinals in each valve, and well-developed laterals), *Microloripes dentatus* is similar to such minute species as *Lucina (Callucina?) sabelli,* an early member of the *Callucina-Parvilucina* complex.

On the other hand, *Loripes lacteus* externally closely resembles *Anodontia alba* (cf. Pl. 35, fig. 4, and Pl. 36, fig. 1), though the latter species is larger and has an external ligament. The obsolescent laterals and single right-valve cardinal of *L. lacteus* recall the Eocene to Miocene species placed in *Eophysema* and *Gardnerella,* some of which may be ancestral to edentulous species of *Anodontia s. s.* Further evidence for a possible relationship between *Loripes* and *Anodontia* is the existence of the Mediterranean species *Loripinus fragilis* (Philippi, 1836), which has an internal ligament but is edentulous. Dall (1901b) considered *Loripinus* Monterosato, 1883, a subgenus of *Anodontia* [as does Chavan (1969)]; but *L. fragilis* also seems similar to *Loripes lacteus.*

### **Loripes (Loripes) lacteus** Poli

Plate 36, figures 1-3

*Loripes lacteus* Poli, 1791, p. 31; Poli, 1795, p. 46, pl. 15, figs. 28-29; Lamy, 1920, pp. 100-106; Thiele, 1935, p. 867.
*Loripes (Loripes) lacteus* Poli, Chavan, 1937, pp. 268-269.
*Amphidesma lucinalis* Lamarck, 1818, p. 491.
*Loripes lucinalis* (Lamarck), Dall, 1901b, p. 803; Dall, 1903, p. 1356; Chavan, 1969, p. *N*496, fig. E4a 1.

*Description.* — Shell small (median length of 32 specimens 14 mm, range 11-20 mm), usually longer than high (median H/L 0.94, range 0.91-1.01), moderately inflated (median D/L 0.26, range 0.22-0.30), anterior expansion moderate to great (median A/L 0.50, range 0.44-0.56). Surface sculpture as in generic diagnosis; thin, yellow-brown periostracum present. All other characters as in generic diagnosis.

*Types.* — I have no information as to the location of Poli's collection.

*Material.* — The phenetic study was based on about 40 Recent specimens, all from the Mediterranean Sea, in the collections of the Yale Peabody Museum.

*Discussion.* — According to Lamy (1920), there has been confusion between *Loripes lacteus* Poli and *Tellina lactea* Linné, 1758. Dall (1903) and Lamy (1920) considered the latter to be a species of *Diplodonta.* Believing *L. lacteus* to be preoccupied, Dall (1901b, 1903) employed Lamarck's (1818) name *Amphidesma lucinalis* for Poli's species. *L. lacteus,* according to Lamy, is found in the Mediterranean, the English Channel, the Bay of Biscay, and the Black Sea.

### Genus **DIVARICELLA**

*Author.* — Von Martens, 1880, p. 321.

*Types species.* — *Lucina (Divaricella) angulifera* von Martens, 1880, p. 321, pl. 22, figs. 14, 14a, by original designation.

*Discussion.* — Von Martens was the first to propose a separate name for the divaricate lucinids. Chavan (1951a), in an intensive study of these forms, recognized 11 taxa (six genera, some subdivided to yield a total of nine subgenera), including six new names. Glibert and van de Poel (1967) proposed the new subfamily name Divaricellinae for the divaricate lucinids. Chavan (1969) used this subfamily name and repeated his earlier classification of the group in the *Treatise on Invertebrate Paleontology.*

The type species of *Divaricella s. s.* is an Indian Ocean form differing from most of the North American species that have been placed in *Divaricella* in having a more reduced dentition, with laterals virtually or completely lacking; a smooth inner ventral margin; and divarications which stand out from the shell surface, producing a coarse sculpture. The North American *Lucina quadrisulcata* d'Orbigny, 1842, which Chavan (1951a) made the type species of a new genus, *Divalinga,* has well-developed laterals, a denticulate ventral margin, and fine surface sculpture.

Chavan (1951a) believed that divaricate surface sculpture distinguishes a phylogenetically distinct group showing evolutionary trends paralleling those in the other lucinid lineages, but he also discussed the possibility that divaricate surface sculpture developed independently within two or more of the non-divaricate groups. Since I have studied in detail only three divaricate species, representing two of the subgenera (in different genera) recognized by Chavan, I shall not speculate on which of the two alternatives is correct. There seems, however, to be no difference of more than subgeneric magnitude between Chavan's *Divalinga (Divalinga),* represented here by *D. (D.) quadrisulcata* and *D. (D.) eburnea,* and his *Divaricella (Egracina),* represented here by *D. (E.) dentata.* Consequently, I have placed both subgenera in *Divaricella,* retaining the subgeneric names proposed by Chavan. I shall give no diagnosis of *Divaricella s. s.* because I have not studied the type species or any species which Chavan considered consubgeneric with it.

*Distribution and phylogenetic relationships.* — Chavan (1969) compiled data on the geographic and stratigraphic distribution of the 11 taxa which he included in the subfamily Divaricellinae. The observed stratigraphic ranges, and the number of taxa having each range, are as follows: Eocene-Oligocene (1); Eocene (2); Oligocene (1); Oligocent-Recent (2); Miocene-Recent (2); Pliocene-Recent (1); Pleistocene-Recent (1); Recent (1). This pattern indicates a fairly distinct separation of the *Divaricella* group into

Paleogene and Neogene faunas. There is also a single Upper Cretaceous (Campanian) species, *Cyclas lanceolata* Stoliczka, 1871, from India, which is divaricate, but which Chavan was unable to assign unequivocally to any of the subgenera of *Divaricella s. l.*

The Recent divaricate lucinids have a world-wide distribution, particularly in warm waters; they have been reported from Europe, the Indo-Pacific, Africa, and both coasts of North and South America.

### Subgenus **DIVALINGA**

*Author.* — Chavan, 1951a, p. 6.

*Type species.* — *Lucina quadrisulcata* d'Orbigny, 1842, p. 294, pl. 27, figs. 34-36, by original designation.

*Discussion.* — Chavan (1951a, 1969) divided *Divalinga* into three subgenera — *Divalinga s. s.*, *Viaderella*, and *Stchepinskya*.

*Diagnosis.* — Shell of small to medium size, slightly elongate to round, moderately to strongly inflated, anterior expansion moderate to great. Surface sculpture divaricate, distinct; growth rings irregularly or regularly spaced, but not deep. Anterior dorsal area faint, forming pseudo-lunule; posterior one usually not set off. Lunule long, narrow, triangular, shallow; strongly asymmetrical, nearly all in right valve. Ligament external. Anterior adductor scar rather short, curved; posterior one elliptical, about as long as anterior one. Hinge plate narrow. Laterals single in right valve, double in left, often obsolescent (particularly posterior ones). Two cardinals in each valve; right anterior cardinal much reduced; right posterior cardinal slightly bifid; cardinals in left valve diverging strongly from each other. Pallial blood vessel scar present. Inner ventral margin denticulate.

*Distribution and phylogenetic relationships.* — *Divaricella (Divalinga) quadrisulcata* (d'Orbigny) is common in the Recent fauna; it is found living from Cape Cod to Brazil. It also occurs as a Pleistocene fossil in southeastern North America. Dall (1903) also recorded it from the Miocene of Virginia, but Chavan (1951a) believed that this form, originally called *Lucina conradi* d'Orbigny, 1852, was not conspecific with the Recent species. The West Coast analogue of *D. (D.) quadrisulcata, D. (D.) eburnea* (Reeve, 1850), is recorded by Grant and Gale (1931) from the Pliocene of western Mexico and Baja California and the Pleistocene of western Mexico and the Galapagos Islands; it is found living from Baja California to Peru (Keen, 1958). Woodring, Bramlette, and Kew (1946) called an early Miocene form from southern California *Divaricella* cf. *eburnea.*

Several Pliocene and Miocene species which are closely similar to *D. (D.) quadrisulcata* are *D. (D.) compsa* Dall, 1903 (Pliocene, Caloosahatchee Formation, Florida); *D. (D.) prevaricata* Guppy, 1896 (middle Miocene, Bowden Formation, Jamaica); *D. (D.) chipolana* Dall, 1903, and *D. (D.) waltonia* Gardner, 1926 (middle Miocene, Alum Bluff Group, Florida); and *D. (D.) comis* Olsson, 1964 (early Miocene, Angostura Formation, Ecuador). *Divaricella subrigaultina* (Meyer, 1886), from the middle Oligocene Vicksburg Group of Mississippi, probably also belongs to *Divalinga;* I have, however, seen only one specimen, an incomplete left valve, of this species.

Two other North American species may also belong to *Divalinga.* One, a late Oligocene species from the Chickasawhay Marl of Florida, called *Divaricella* sp. by Mansfield (1940), is known only from an external mold; in size and sculpture it resembles small individuals of *D. (D.) quadrisulcata.* Richards (1953) described *Divaricella robertsi* from the upper Eocene Moodys Branch Formation of Florida. He compared it to *D. ermenovillensis* (d'Orbigny), an upper Eocene species from the Paris Basin which Chavan (1951a) referred to *Boeuvia* Chavan, 1948 (= ? *Bourdotia* Dall, 1901b). From Richards' figure, however, the Florida species seems to be too poorly preserved for even its placement in *Divaricella s. l.* to be certain.

A species from the early and middle Eocene of France, *Lucina rigaultiana* Deshayes, 1860, the type species of *Stchepinskya* Chavan, 1951a, is probably related to the North American species of *Divalinga,* differing from them principally in its smaller size. The small, curved anterior adductor scar of *Stchepinskya* and *Divalinga* is reminiscent of that of *Parvilucina* and of the small Eocene species probably ancestral to it.

Grant and Gale (1931) believed that *Divaricella* might belong to the Ungulinidae rather than to the Lucinidae. In several respects — the orbicular, inflated shell with approximately central beaks; the short anterior adductor; and the tendency of the cardinal teeth to diverge from each other rather than to be roughly parallel — the species of *Divalinga* do resemble species of the Ungulinidae. Allen (1958), however, who studied the anatomy of *D. (Divalinga) quadrisulcata,* pronounced it to be a member of the Lucinidae.

### **Divaricella (Divalinga) quadrisulcata** (d'Orbigny)

Plate 36, figures 4-7

*Lucina divaricata* Lamarck, 1818, p. 541 [part]; Say, 1824, p. 148; Conrad, 1840, p. 39, pl. 20, fig. 3; Tuomey and Holmes, 1857, p. 59, pl. 17, figs. 10-11; Holmes, 1860, p. 27, pl. 6, fig. 1.

*Lucina quadrisulcata* d'Orbigny, 1842, p. 294, pl. 27, figs. 34-36; d'Orbigny, 1846, p. 584.

*Divaricella quadrisulcata* (d'Orbigny), Dall, 1901b, p. 815; Dall, 1903,

pp. 1389-1390; Lamy, 1920, pp. 267-270, fig.; Abbott, 1954, p. 391, pl. 30m; Warmke and Abbott, 1961, p. 179, pl. 36L.
*Divalinga (Divalinga) quadrisulcata* (d'Orbigny), Chavan, 1951a, pp. 6-7, figs. 3-4; Chavan, 1969, p. *N*506, fig. E12, 9a, 9b.
? *Lucina conradi* d'Orbigny, 1852, p. 117, pl. 21, fig. 94.

*Description.* — Shell of small to medium size (median length of 29 specimens 17 mm, range 8-23 mm), generally slightly longer than high (median H/L 0.95, range 0.92-1.02), strongly inflated (median D/L 0.32, range 0.29-0.35), anterior expansion moderate to great (median A/L 0.50, range 0.42-0.56). Sculpture, dorsal areas, lunule, ligament, dentition, musculature, and other internal features as in generic diagnosis. Shell exterior reddish-brown or gray in specimens from northern localities, white in southern ones.

*Types.* — The original specimens of *Lucina quadrisulcata,* if still extant, are presumably in the d'Orbigny collection in the British Museum (Natural History) (Dance, 1966).

*Material.* — The phenetic study was based on about 40 Recent specimens, from Massachusetts, New Jersey, Bermuda, Florida, and the Caribbean, in the Yale Peabody Museum collections.

*Discussion.* — This is one of the widest-ranging latitudinally of lucinid species; Dall (1901b) reported that it is found living from Massachusetts to Brazil. Allen (1958) collected it in shallow water (about 5 feet deep) in Florida and the Bahamas; Stanley (1970) said that it lives on moderately exposed intertidal flats in Florida and in a back-reef environment in Puerto Rico. It inhabits cleaner and coarser sands than do most Caribbean lucinids, and Stanley (1969, 1970) showed that the divaricate ridges apparently act as a rasp, facilitating burrowing into sandy substrata. Several Recent species of the non-lucinoid superfamily Tellinacea have divaricate ridges which are used in a similar manner (Stanley, 1969, 1970). The depth preference of *D. (D.) quadrisulcata* apparently does not change appreciably from north to south, perhaps because the species is so rigorously adapted to fairly coarse substrata, but there is a noteworthy latitudinal change in its coloration, with the more northerly individuals having darker-colored shells. Cold-water bivalves are commonly dark-colored or have a brown periostracum, whereas white and brightly colored species are most frequently found in the tropics.

Dall (1901b) synonymized the Miocene species *Lucina conradi* d'Orbigny, 1852, from Virginia, with *D. (D.) quadrisulcata,* but Chavan (1951a) believed them to be distinct. It it also possible that *L. conradi* is synonymous with one of the Floridian Miocene species of *Divalinga.*

Many early European and North American taxonomists used the name *Lucina divaricata* (Linné, 1758) for all divaricate species, including *D. (D.) quadrisulcata* and *D. (Egracina) dentata.* Dall (1903, pp. 1389-1390), in a fuller synonymy that that given here, attempted to clarify the nomenclature but remarked that in many cases the synonymy "cannot be disentangled without more trouble than it is worth". Actually, *Tellina divaricata* Linné is a Recent Mediterranean species which has an inset ligament; it is the type species of *Lucinella* Monterosato, 1883.

### **Divaricella (Divalinga) eburnea** (Reeve)

Plate 36, figures 8-10

*Lucina eburnea* Reeve, 1850, pl. 8, fig. 49.
*Divaricella eburnea* (Reeve), Dall, 1901b, p. 815; Lamy, 1920, pp. 273-274.
*Divaricella dentata* var. *eburnea* (Reeve), Grant and Gale, 1931, pp. 296-297, pl. 14, figs. 1a, 1b.
*Divalinga (Divalinga) eburnea* (Reeve), Chavan, 1951a, p. 6; Keen, 1958, pp. 100-101, fig. 206.
*Divaricella lucasana* Dall and Ochsner, 1928, p. 122.

*Description.* — Shell of small to medium size (median length of 13 specimens 19 mm, range 9-24 mm), slightly longer than high (median H/L 0.96, range 0.92-1.02), moderately to strongly inflated (median D/L 0.29, range 0.26-0.43), anterior expansion usually moderate (median A/L 0.48, range 0.45-0.51). Other features of shell as in *D. (D.) quadrisulcata,* except all specimens white in color.

*Types.* — Reeve's description of *Lucina eburnea* was based on specimens in the collection of Hugh Cuming, now housed in the British Museum (Natural History) (Dance, 1966).

*Material.* — The phenetic study was based on about 15 Recent specimens, all from Baja California, in the Yale Peabody Museum collections.

*Discussion.* — Dall and Ochsner (1928) considered the name *Lucina eburnea* Reeve preoccupied by *L. eburnea* Deshayes, 1835, and proposed *Divaricella lucasana* as a replacement name. According to Grant and Gale (1931), however, Deshayes's name is a *nomen nudum* in a list, and thus Reeve's name can be used.

Grant and Gale (1931) considered *D. (D.) eburnea* a variety of *D. (Egracina) dentata* (Wood, 1815), and believed that *D. (D.) quadrisulcata* and *D. (D.) eburnea* might be synonymous. As with other species pairs from opposite sides of the Isthmus of Panama, however, I have treated *quadrisulcata* and *eburnea* as specifically distinct. Reasons for placing *D. (E.) dentata* and *D. (D.) quadrisulcata* in different subgenera are given in the discussion of the former species.

The present range of *D. (D.) eburnea* is from southern

Baja California to Peru (Keen, 1958). Its maximum recorded northern extent, in Pliocene time, was to just north of the California-Baja California boundary (Grant and Gale, 1931). Apparently, unlike its East Coast counterpart *D. (D.) quadrisulcata,* it has remained restricted to warm water.

### Subgenus **EGRACINA**

*Author.* — Chavan, 1951a, p. 20.

*Type species.* — *Divaricella (Egracina) dentata* var. *collignoni* Chavan, 1951a, pp. 20-21, figs. 23, 24, 24bis, by original designation.

*Discussion.* — Chavan proposed *Egracina* as a subgenus of *Divaricella,* which he considered generically distinct from *Divalinga.* The type species is a Recent African taxon (the holotype is from the Iles Glorieuses, northwest of Madagascar) which Chavan believed to be a "variety" of the Caribbean *D. (E.) dentata* (Wood, 1815).

*Diagnosis.* — Shell of medium size, longer than high, moderately to strongly inflated, anterior expansion moderate. Sculpture divaricate, with growth rings generally deep and regularly spaced. Terminations of divarications form dorsal spines, particularly on posterior margin. Anterior adductor scar of normal length, narrow, curved away from pallial line; posterior adductor scar elliptical; pedal retractor scars not evident. Hinge plate narrow. Anterior laterals absent; posterior laterals single in both valves, obsolescent. Two cardinals in each valve; right anterior cardinal partly effaced by deep lunule; right posterior cardinal slightly bifid; cardinals in left valve not divergent. Pallial blood vessel scar present. Inner ventral margin not denticulate; terminations of divaricate ribs give it serrate appearance (Pl. 36, figs. 12, 13).

*Distribution and phylogenetic relationships.* — According to Chavan (1951a), living representatives of *Egracina* occur on the eastern and western coasts of Africa and in the Caribbean. Apparently the only fossil representatives are from the Pleistocene of Santo Domingo, belonging to *D. (E.) dentata* (Wood) (Dall, 1903). All the Pliocene and earlier species of *Divaricella* in North America seem more similar to *D. (Divalinga) quadrisulcata* than to *D. (E.) dentata. Divaricella s. s.*, to which *Egracina* is presumably most closely related, is recorded only from Pliocene to Recent time in the Indio-Pacific region. Chavan (1951a) did not speculate on possible relationships of *Divaricella s. s.* and *Egracina,* either to the other divaricate subgenera or to the nondivaricate groups. *D. (E.) dentata* may have been derived from a late Tertiary species of *Divalinga* by loss of the lateral teeth, lengthening of the anterior adductor, and increase in the prominence and regularity of the growth rings. I consider only a subgeneric separation of *Egracina* and *Divalinga* to be appropriate.

### **Divaricella (Egracina) dentata** (Wood)

Plate 36, figures 11-13

*Tellina dentata* Wood, 1815, pp. 195-196, pl. 46, fig. 7.
*Divaricella dentata* (Wood), Dall, 1901b, p. 815; Dall, 1903, pp. 1390-1391; Lamy, 1920, pp. 275-276; Abbott, 1954, p. 391; Warmke and Abbott, 1961, p. 179.
*Divaricella (Egracina) dentata* (Wood), Chavan, 1951a, p. 20.
*Lucina divaricata* Reeve, 1850, pl. 8, fig. 47a [*non Tellina divaricata* Linné, 1758; *nec Lucina divaricata* Lamarck, 1818].

*Description.* — Shell medium-sized (median length of 24 specimens 26 mm, range 12-29 mm), longer than high (median H/L 0.94, range 0.92-0.97), moderately to strongly inflated (median D/L 0.28, range 0.25-0.31), anterior expansion moderate (mediate A/L 0.46, range 0.42-0.50). All other features as in generic diagnosis. Growth rings generally regularly spaced, deep; divarications are offset by growth rings, resembling faulted strata (Pl. 36, fig. 11); in contrast, divarications in species of *Divalinga* are continuous across growth rings.

*Types.* — Wood (1815) stated that the shell on which his description of *Tellina dentata* was based was "in the cabinet of Mrs. Mawe". Many of the shells in the Mawe collection were sold to other collectors (Dance, 1966), and no information on the disposal of the type of *T. dentata* is available.

*Material.* — The phenetic study was based on about 25 Recent specimens, from Florida, Bermuda, and the West Indies, in the collections of the Yale Peabody Museum.

*Discussion.* — Warmke and Abbott (1961) considered *D. (E.) dentata* to be "probably only a form" of *D. (Divalinga) quadrisulcata.* The differences in size, lunule, musculature, and lateral dentition, however, seem to be sufficiently great that the species should be considered subgenerically distinct. *D. (E.) dentata,* unlike *D. (D.) quadrisulcata,* is apparently confined to warm waters.

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## PLATES

Abbreviations used in explanations:

YPM-IP—Division of Invertebrate Paleontology, Peabody Museum of Natural History, Yale University, New Haven, Conn.

YPM-IZ—Division of Invertebrate Zoology, Peabody Museum of Natural History, Yale University, New Haven, Conn.

USNM—U.S. National Museum of Natural History, Washington, D.C.

All illustrated specimens with YPM numbers are deposited in the Yale Peabody Museum. Magnifications are given in linear dimensions and are the same for all views of a given specimen unless otherwise noted. Numbers on figured specimens do not always correspond to the specimen numbers given in the plate explanations, since the specimens were individually renumbered after having been photographed.

## EXPLANATION OF PLATE 25

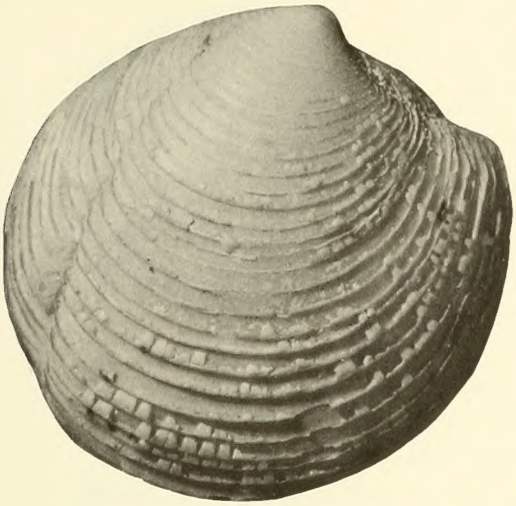
*Figure* *Page*

1-4. *Lucina (Lucina) pensylvanica* (Linné) ........ 250

1. Exterior of right valve. Recent, Abaco Cay, Bahamas. YPM-IZ 8734. (×2). 2. Interior of Fig. 1. 3. Interior of left valve of same specimen. 4. Front view of bivalved specimen showing "figure-8" lunule (small indented area under enrolled beaks) and anterior dorsal area (large heart-shaped area in front of beaks). Recent, Clearwater Bay, Florida YPM-IZ 8735. (×4).

5-10. *Lucina (Here) excavata* Carpenter ........ 252

5. Exterior of right valve. Recent, San Diego, California. USNM 73651. (×2). 6. Interior of left valve of same specimen. 7. Interior of Fig. 5. 8. Front view of both valves in articulation; note large lunule and weakly defined anterior dorsal area. 9. Exterior of right valve of juvenile specimen, figured by Dall (1901b); compare with Fig. 5 and note ontogenetic changes in degree of inflation and in relative size of the lunule. Recent, Santa Catalina Island, California. USNM 108828. (×4). 10. Interior of Fig. 9.



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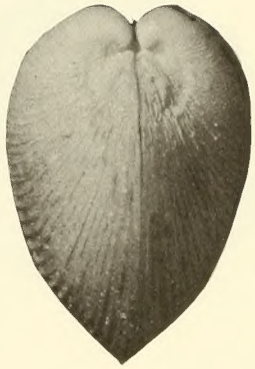

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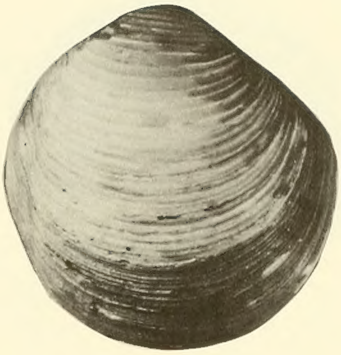

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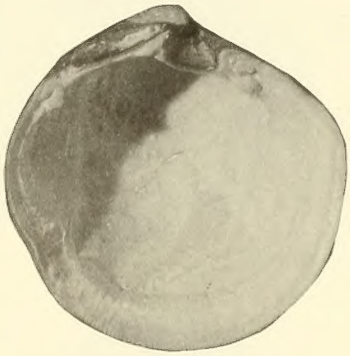

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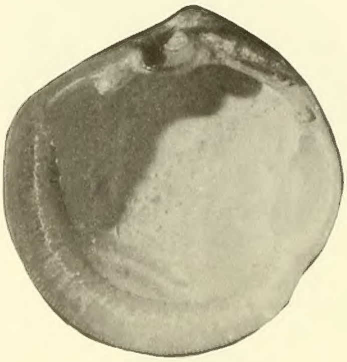

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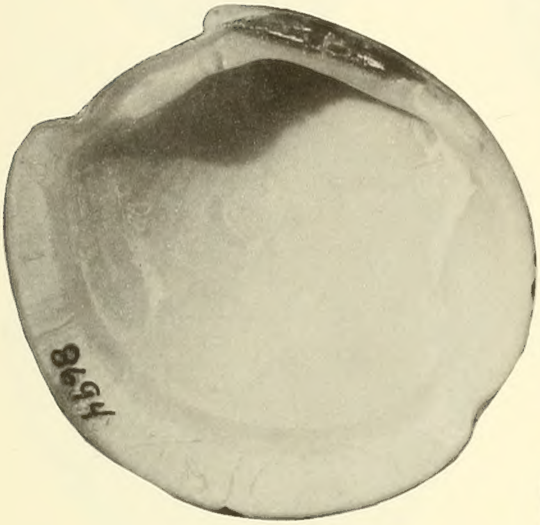

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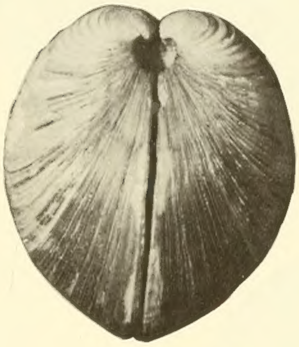

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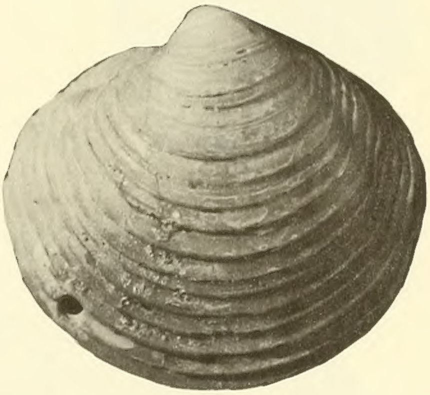

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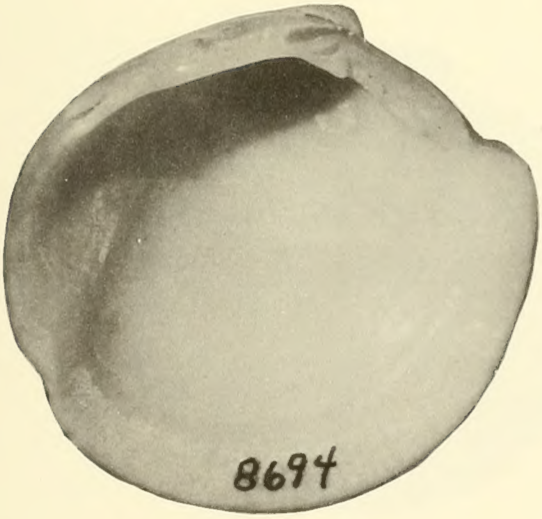

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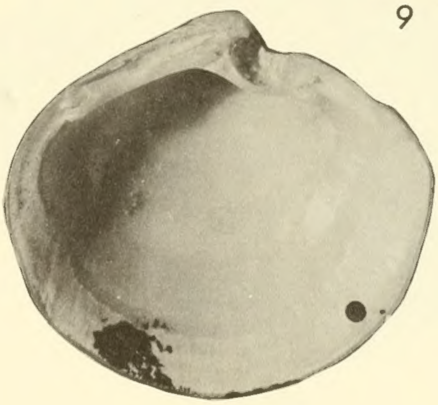

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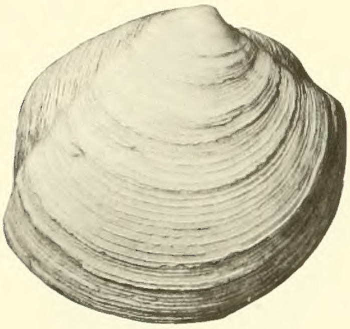
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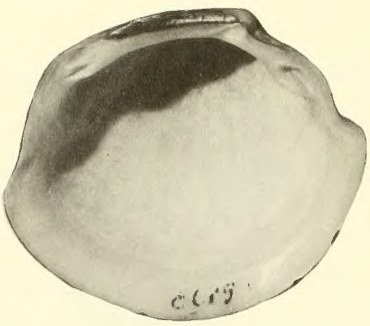
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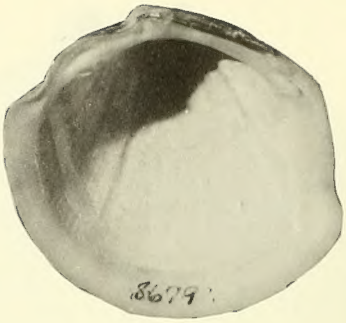

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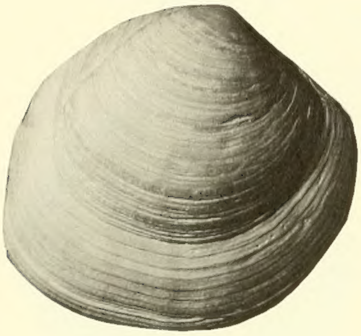
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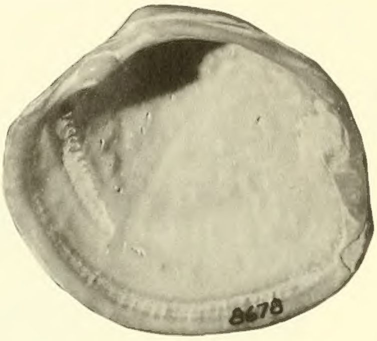

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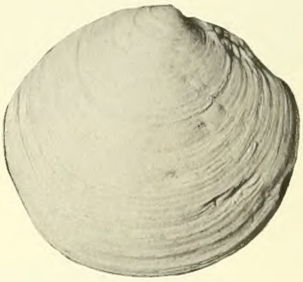
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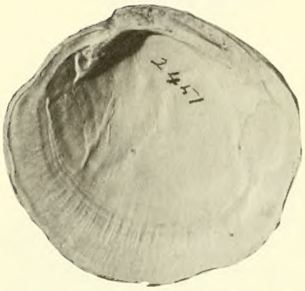

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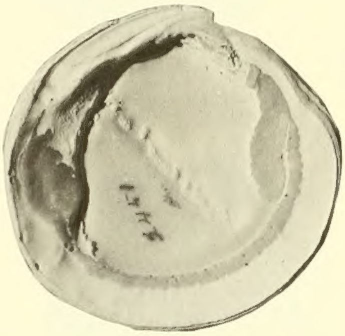

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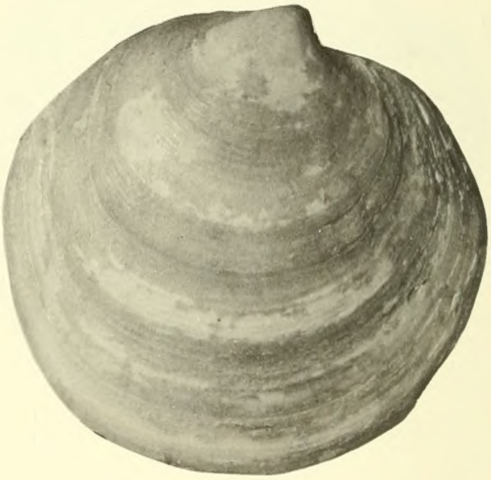
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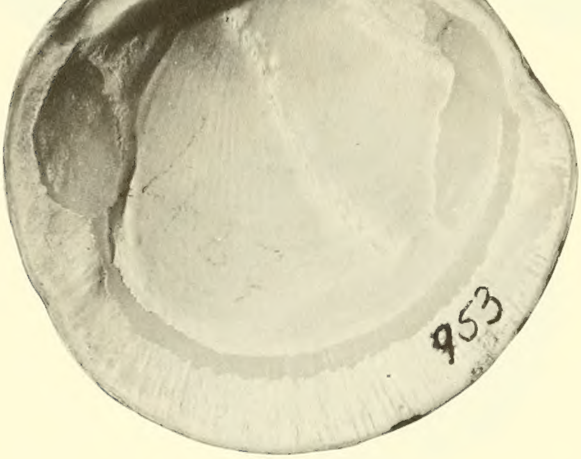

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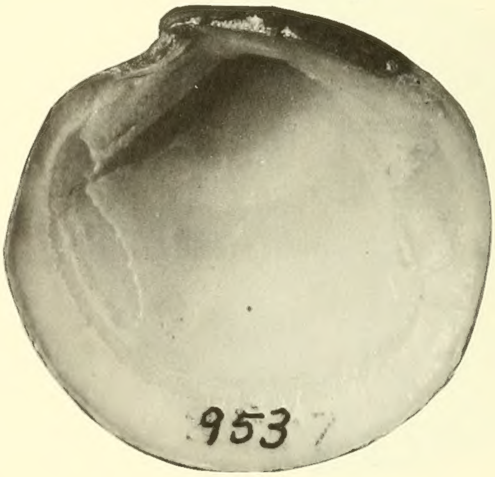

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## EXPLANATION OF PLATE 26

*Figure* *Page*

1-5. *Lucina (Phacoides) pectinata* (Gmelin) ........ 254

1. Exterior of right valve. Recent, West Indies. YPM-IZ 8736. (×1). 2. Interior of left valve of same specimen, showing "normal" dentition and musculature. 3. Interior of Fig. 1. 4. Exterior of right valve. Recent, Florida. YPM-IZ 8737. (×1). 5. Interior of Fig. 4, showing variant form of dentition and musculature [see text].

6-8. *Lucina (Stewartia) anodonta* Say ........ 256

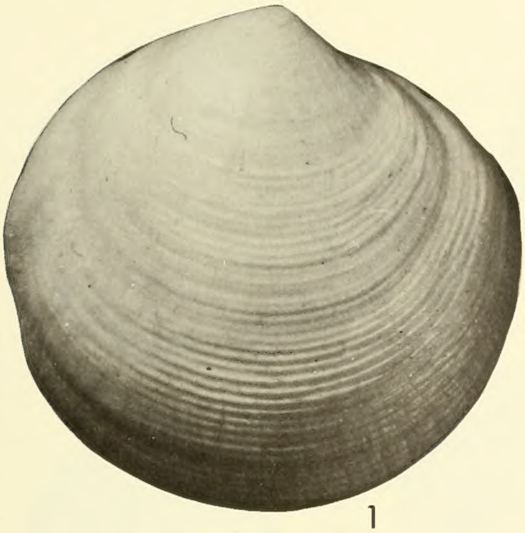
6. Exterior of right valve. Miocene, probably Choptank Formation, Jones Wharf, Maryland. YPM-IP 27051. (×1). 7. Interior of Fig. 6. 8. Interior of left valve from same locality. YPM-IP 27052. (×1).

9-11. *Lucina (Stewartia) floridana* Conrad ........ 257

9. Exterior of right valve. Recent, Egmont Key, Florida. YPM-IZ 8738. (×1). 10. Interior of left valve from same locality. YPM-IZ 8739. (×1). 11. Interior of Fig. 9.

## EXPLANATION OF PLATE 27

| Figure | | Page |
|---|---|---|
| 1-4. | *Lucina (Callucina) radians* Conrad | 258 |
| | 1. Exterior of right valve. Recent, Santa Rosa Island, Florida. YPM-IZ 8740. (×4). 2. Interior of left valve from same locality. YPM-IZ 8741. (×4). 3. Interior of Fig. 1. 4. Top view of bivalved specimen from same locality, showing triangular, asymmetrical lunule. YPM-IZ 8742. (×4). | |
| 5-7. | *Lucina (Callucina) papyracea* Conrad | 259 |
| | 5. Exterior of right valve. Middle Eocene, Gosport Sand, Claiborne, Alabama. YPM-IP 27053. (×8). 6. Interior of Fig. 5. 7. Interior of left valve from same locality. YPM-IP 27054. (×8). | |
| 8-13. | *Lucina (Parvilucina) tenuisculpta* Carpenter | 262 |
| | 8. Exterior of right valve. Recent, Kasa-an Bay, Alaska, USNM 226078a. (×4). 9. Interior of left valve from same locality. USNM 226079b. (×4). 10. Interior of right valve from same locality. USNM 226079c. (×4). 11. Exterior of right valve of holotype. Recent, Vancouver Island, British Columbia, USNM 5244. (×4). 12. Interior of left valve of holotype. 13. Interior of right valve of holotype. | |
| 14-16. | *Lucina (Parvilucina) multilineata* Tuomey and Holmes | 263 |
| | 14. Exterior of right valve. Recent, U.S. Fish Commission Station 2277 (35°20'50" N, 75°19'50" W, about 35 mi. east of Savannah, Georgia). YPM-IZ 8743. (×4). 15. Interior of left valve from same locality. YPM-IZ 8744. (×4). 16. Interior of Fig. 14. | |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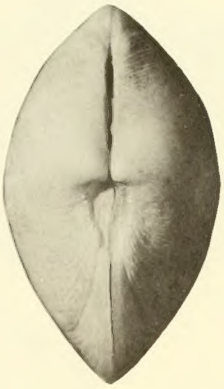
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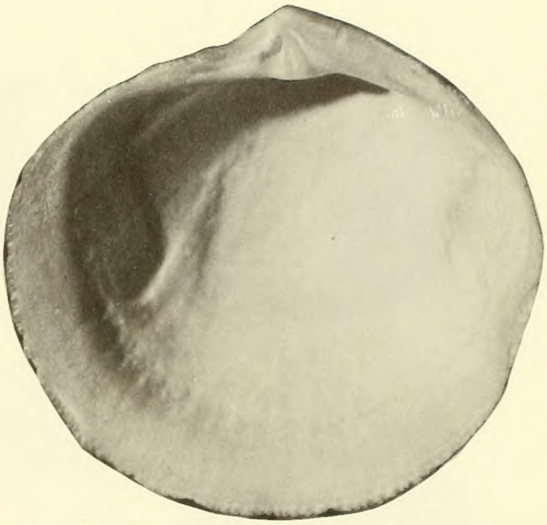
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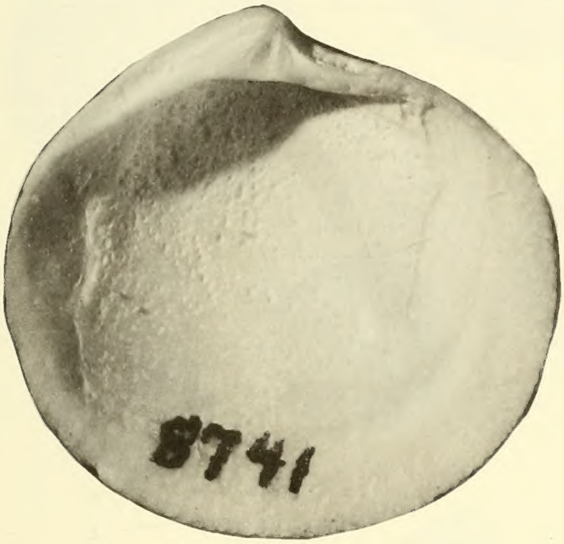

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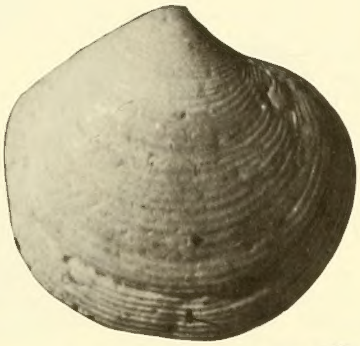
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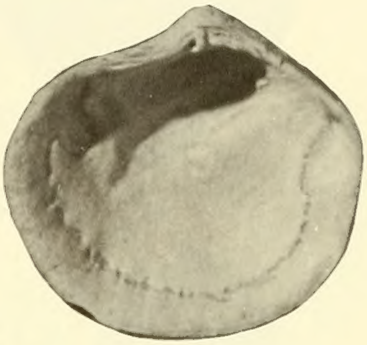
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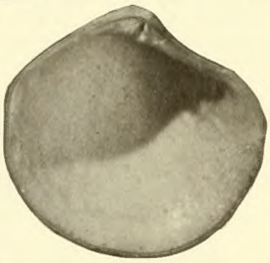
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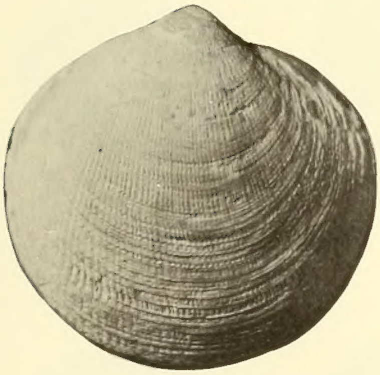
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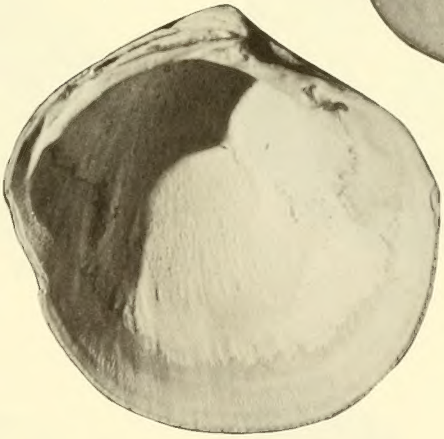
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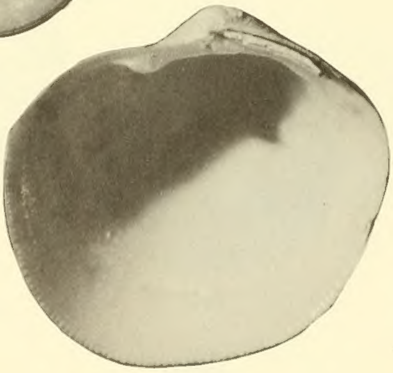
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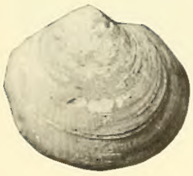
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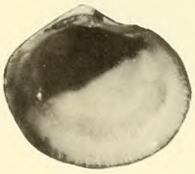
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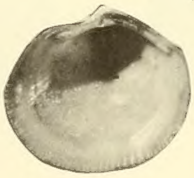
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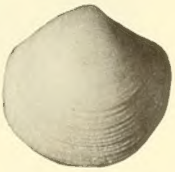
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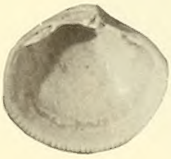
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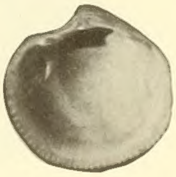
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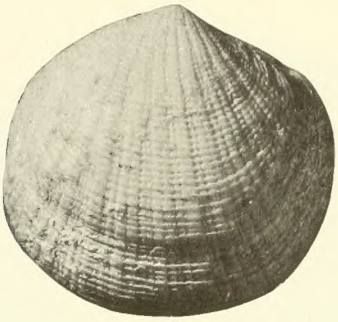
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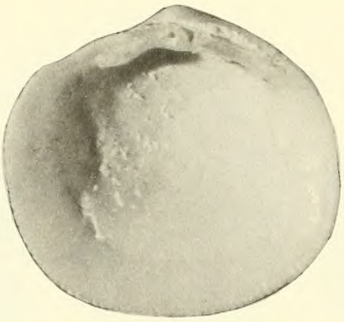
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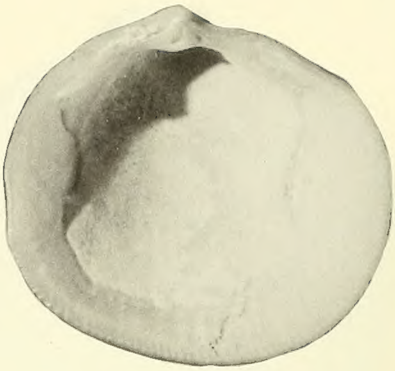
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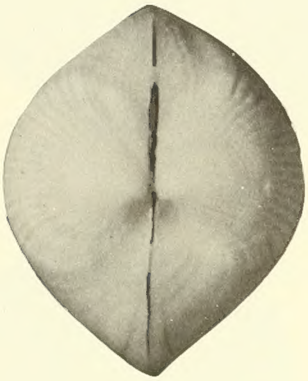
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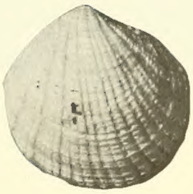
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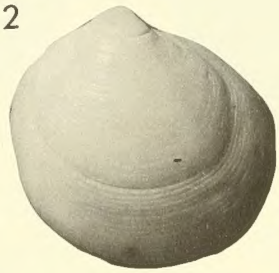
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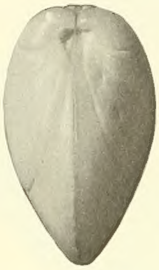
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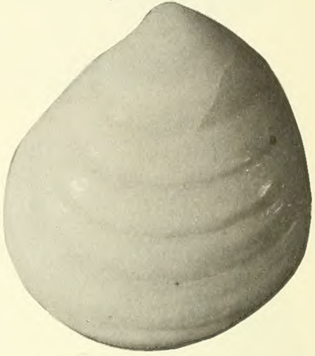
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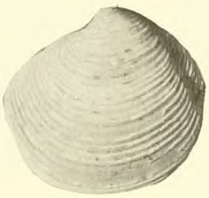
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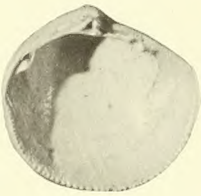
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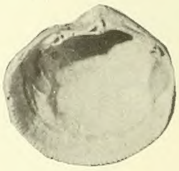
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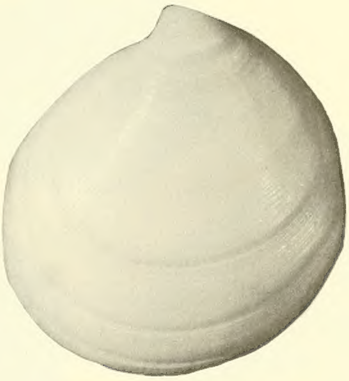
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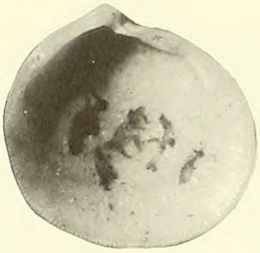
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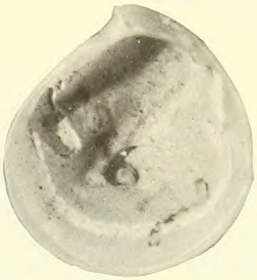
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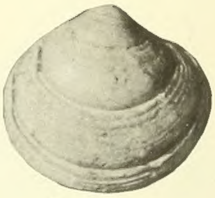
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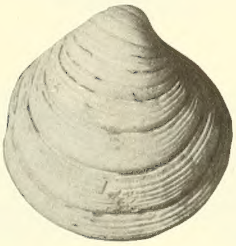
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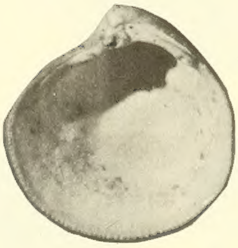
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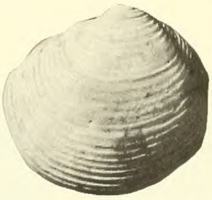
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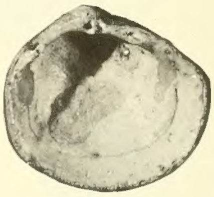
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## EXPLANATION OF PLATE 28

*Figure* *Page*

1-5. *Lucina (Parvilucina?) costata* d'Orbigny ........ 263

1. Exterior of right valve. Recent, Hungry Bay, Bermuda. YPM-IZ 8746. (×4). 2. Interior of Fig. 1. 3. Interior of left valve from same locality. YPM-IZ 8747. (×4). 4. Top view of bivalved specimen. Recent, Negril Beach, Jamaica. YPM-IZ 8748. (×4). 5. Exterior of right valve of juvenile specimen. Recent, Hungry Bay, Bermuda. YPM-IZ 8745. (×4).

6-15. *Lucina (Cavilinga) trisulcata* Conrad ........ 266

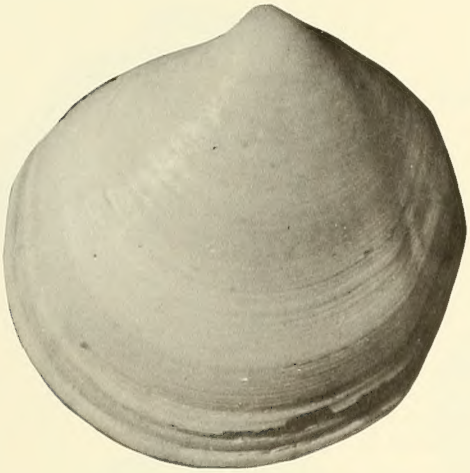
6. Copy (×2) of Conrad's (1845) figure of *Lucina trisulcata.* Original magnification unknown. Conrad's specimen was from the upper Miocene Duplin Marl, from either the Natural Well [southwest of Magnolia], Duplin County, North Carolina, or the Neuse River, N.C. [see text]. 7. Exterior of right valve. Recent, West Indies. USNM 130492a. (×4). 8. Same specimen as fig. 7; front view of both valves in articulation. 9. Exterior of left valve from same lot; contrast with fig. 7 for evaluation of degree of difference in shape and in development of growth rings in Recent specimens of *L. (C.) trisulcata.* USNM 130492b. (×4). 10. Exterior of left valve of specimen corresponding in shape, size, and sculpture to *"Phacoides (Cavilucina) trisulcatus* var. *whitfieldi"* Dall and *"Phacoides (Parvilucina) prunus"* Dall. Middle Miocene, Calvert Formation, Camp Roosevelt, Maryland. YPM-IP 27055. (×4). 11. Interior of fig. 10. 12. Interior of right valve from same locality. YPM-IP 27056. (×4). 13. Exterior of left valve, one of three syntypes of *Phacoides trisulcatus* var. *blandus* Dall. This is the specimen figured by Dall and Simpson (1901). Recent, San Juan Harbor, Puerto Rico. USNM 17677a. (×4). 14. Interior of left valve, the second syntype of *P. trisulcatus* var. *blandus.* USNM 17677b. 15. Interior of right valve, the third syntype of *P. trisulcatus* var. *blandus.* USNM 17677c.

16-20. *Lucina (Cavilinga) pomilia* Conrad ........ 269

16. Exterior of right valve corresponding in shape and sculpture to *Lucina pomilia* Conrad. Upper middle Eocene, Gosport Sand, Claiborne, Alabama. YPM-IP 27057. (×4). 17. Exterior of right valve corresponding in shape and sculpture to *Lucina alveata* Conrad; same locality as Fig. 16. YPM-IP 27058. (×4). 18. Interior of Fig. 17. 19. Exterior of left valve corresponding in shape and sculpture to *Lucina smithi* Meyer; same locality as Fig. 16. YPM-IP 27059. (×4). 20. Interior of Fig. 19.

## EXPLANATION OF PLATE 29

| *Figure* | | *Page* |
|---|---|---|
| 1-3. | *Lucina (Cavilinga) lingualis* Carpenter<br>1. Exterior of left valve. Recent, Gulf of California. YPM-IZ 8749. (×4). 2. Interior of Fig. 1. 3. Interior of right valve of same specimen. | 270 |
| 4-6. | *Lucina (Cavilinga) lampra* (Dall)<br>4. Exterior of right valve. Recent, Gulf of California. YPM-IZ 8750. (×4). 5. Interior of left valve of same specimen. 6. Interior of Fig. 6. | 271 |
| 7-10. | *Lucina (Bellucina) amiantus* (Dall)<br>7. Exterior of right valve of adult specimen. Recent, Clearwater Bay, Florida. YPM-IZ 9072. (×8). 8. Exterior of right valve of juvenile specimen. Recent, Captiva, Florida. YPM-IZ 9071. (×8). 9. Interior of left valve of same specimen. 10. Interior of Fig. 8. | 273 |
| 11-14. | *Lucina (Lucinisca) nassula* Conrad<br>11. Exterior of right valve. Recent, near Longboat Pass, Captiva, Florida. YPM-IZ 9073. (×4). 12. Interior of Fig. 11. 13. Interior of left valve of same specimen. 14. Top view of both valves in articulation, showing short, wide lunule and conspicuous anterior dorsal area. | 275 |
| 15-18. | *Lucina (Lucinisca) nuttalli* Conrad<br>15. Exterior of right valve. Pleistocene, Dead Man Island, San Pedro, California. YPM-IP 27060. (×2). 16. Interior of left valve. Recent, San Diego, California. YM-IZ 9074 (×2). 17. Interior of right valve of same specimen. 18. Same specimen as Fig. 15; top view of both valves in articulation, showing long, triangular lunule. | 276 |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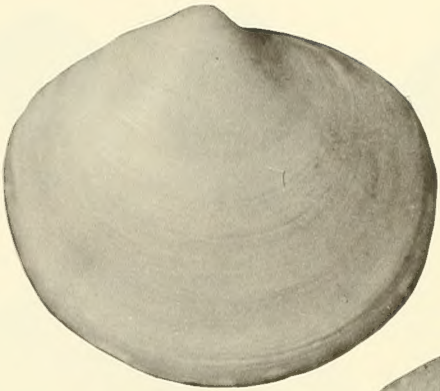
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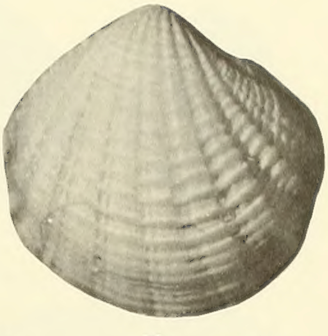
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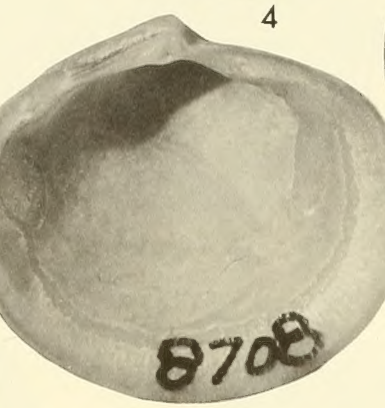

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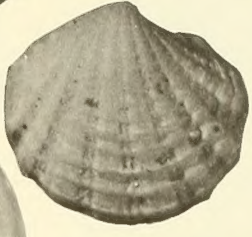
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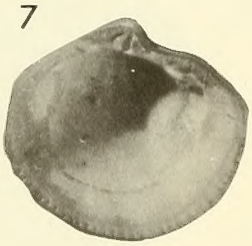
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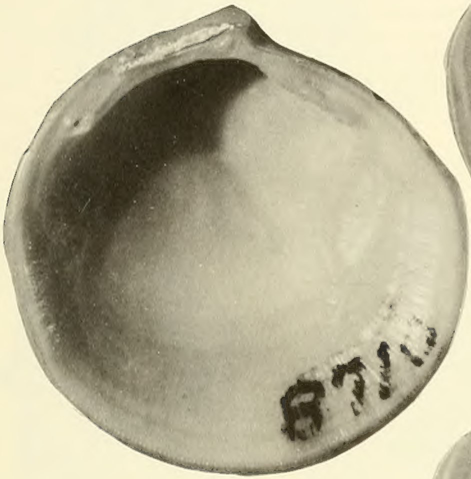

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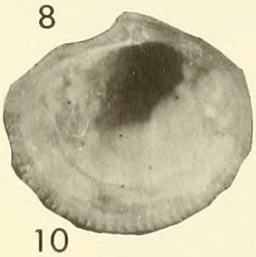
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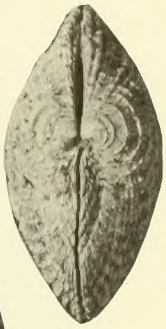
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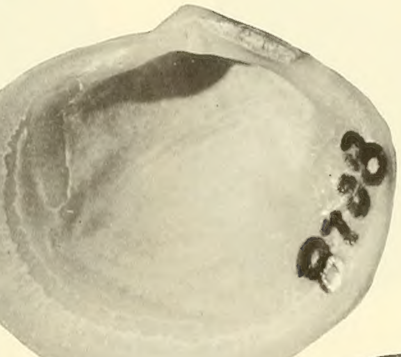

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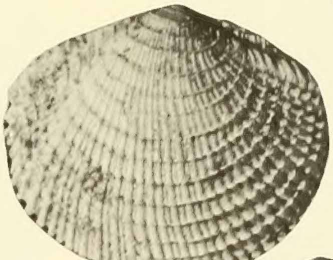
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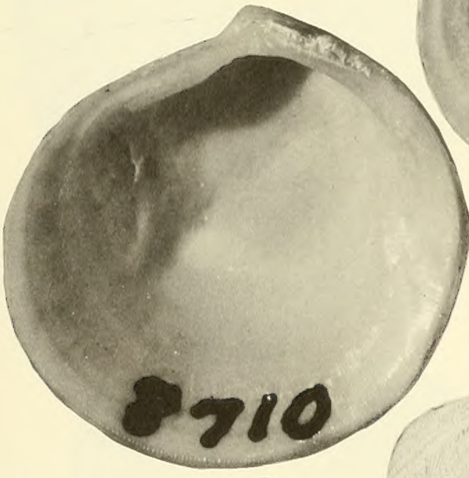

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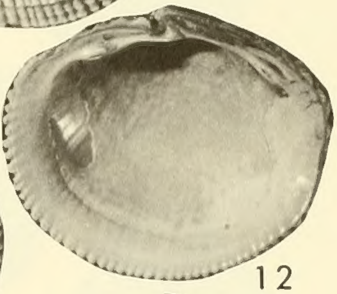
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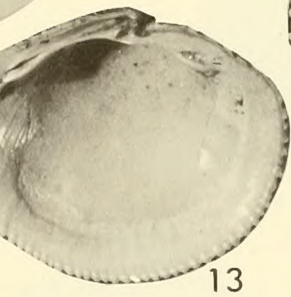
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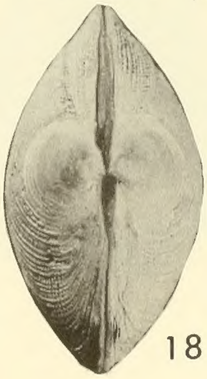
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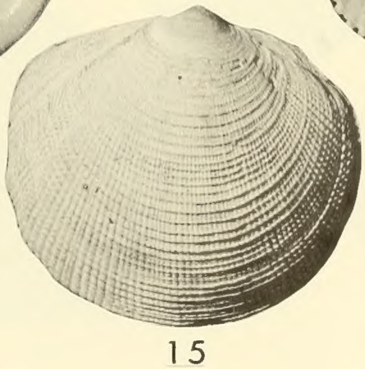
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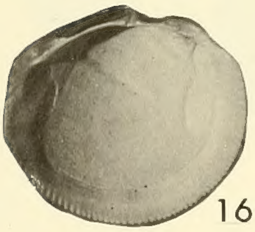
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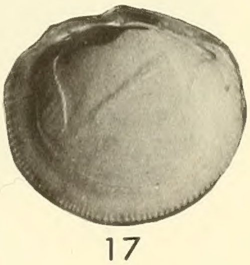
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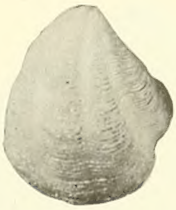
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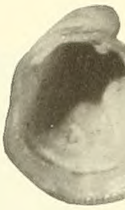
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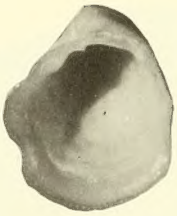
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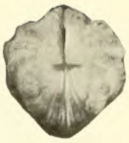
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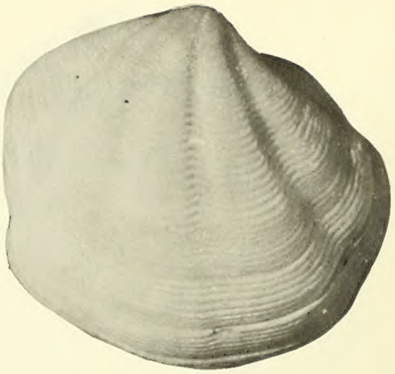
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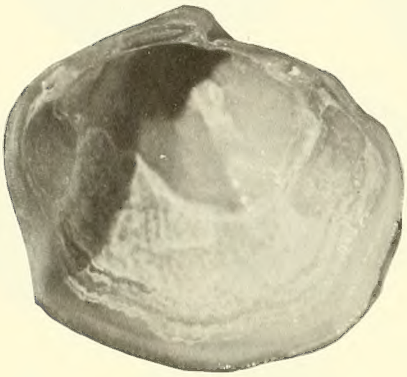
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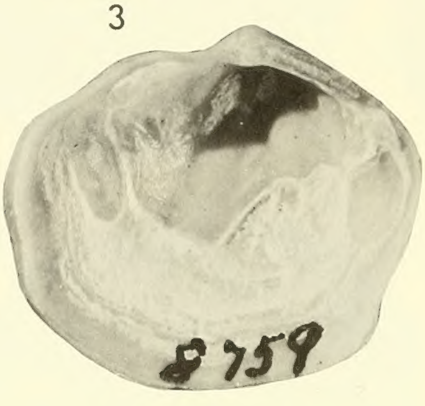

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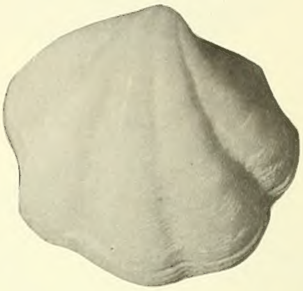
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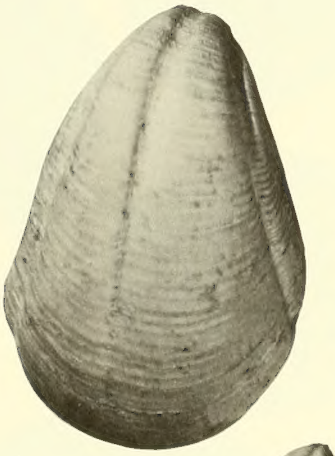
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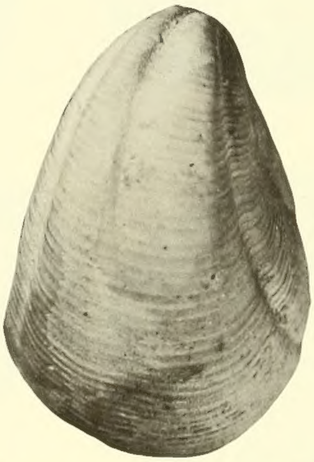
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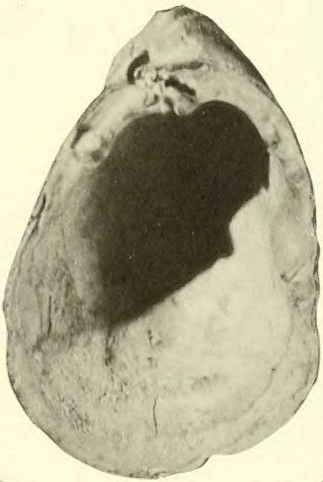
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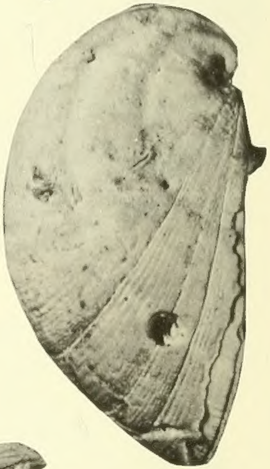
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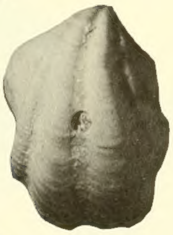
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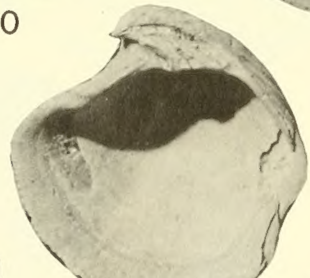
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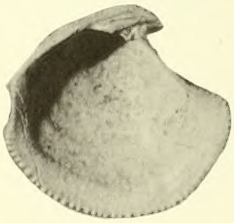
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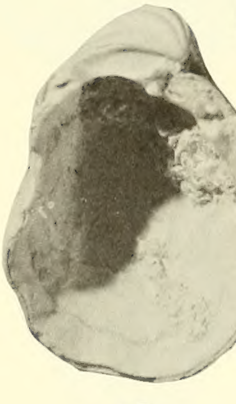
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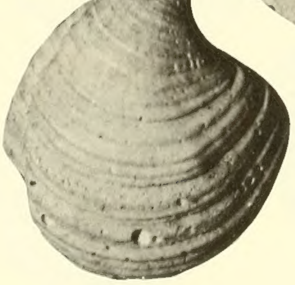
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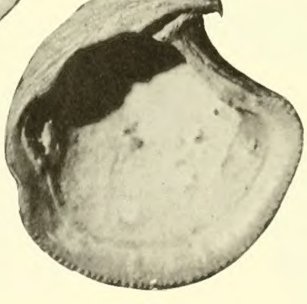
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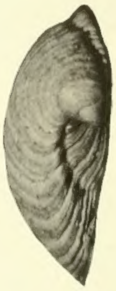
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## EXPLANATION OF PLATE 30

| Figure | | Page |
|---|---|---|
| 1-4. | *Lucina (Pleurolucina) leucocyma* Dall<br>1. Exterior of right valve. Recent, Delroy Tank, Palm Beach County, Florida. YPM-IZ 9075. (×4). 2. Interior of left valve of same specimen. 3. Interior of Fig. 1. 4. Top view of bivalved specimen from same locality. YPM-IZ 9076. (×4). | 277 |
| 5-8. | *Lucina (Pleurolucina) undatoides* Hertlein and Strong<br>5. Exterior of right valve. Recent, La Paz, Baja California. YPM-IZ 9078. (×4). 6. Interior of left valve of same specimen. 7. Interior of Fig. 5. 8. Exterior of right valve of juvenile specimen from same locality. YPM-IZ 9077. (×4) | 278 |
| 9-14. | *Lucina (Pleurolucina) amabilis* Dall<br>9. Exterior of right valve, one of two specimens figured by Dall (1898). Pliocene, Caloosahatchee Formation, Shell Creek, Florida. USNM 147806a. (×4). 10. Exterior of right valve, the second specimen figured by Dall (1898); same locality as Fig. 9. USNM 157806b. (×4). 11. Interior of Fig. 9. 12. Front view of left valve, one of syntypes from same locality as figured specimens. USNM 157806c. (×4). 13. Interior of left valve, a second unfigured syntype. USNM 157806d. (×4). 14. Exterior of right valve of juvenile specimen from same locality. USNM 157805. (×4). | 278 |
| 15-19. | *Lucina? (Recurvella) dolabra* Conrad<br>15. Exterior of right valve. Middle Eocene, Gosport Sand, Claiborne, Alabama. USNM 129643a. (×4). 16. Interior of Fig. 15. 17. Interior of left valve from same locality. USNM 129643b. (×4). 18. Interior of a second left valve from same locality; compare position of anterior adductor of this specimen and of that of Fig. 17. USNM 129643c. (×4). 19. Top view of Fig. 15; note conspicuous anterior dorsal area and lack of true lunule. | 279 |

## EXPLANATION OF PLATE 31

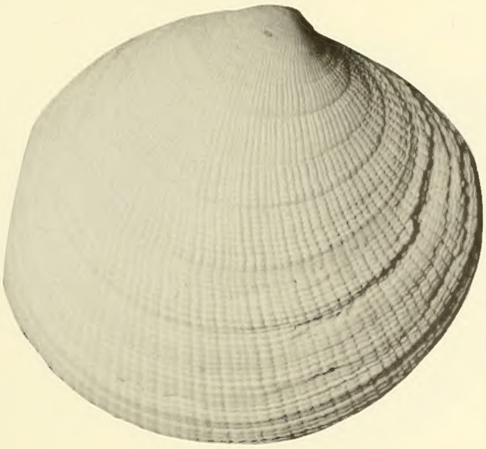
*Figure* *Page*

1-5. *Codakia (Codakia) orbicularis* (Linné) ........ 281

1. Exterior of right valve. Recent, Jamaica. YPM-IZ 9079. (×1). 2. Interior of Fig. 1. 3. Interior of left valve of same specimen. 4. Exterior of left valve of juvenile specimen; comparison with Fig. 1 illustrates ontogenetic decrease in anterior expansion. Recent, Lower Matecumbe Key, Florida. YPM-IP 27061. (×1). 5. Top view of specimen shown in Figs. 1-3, showing short, triangular lunule. (×1).

6, 7. *Codakia (Codakia) distinguenda* (Tryon) ........ 282

6. Exterior of left valve. Recent, La Paz, Baja California. YPM-IZ 9080. (×1). 7. Interior of a second left valve from same locality. YPM-IZ 9081. (×1).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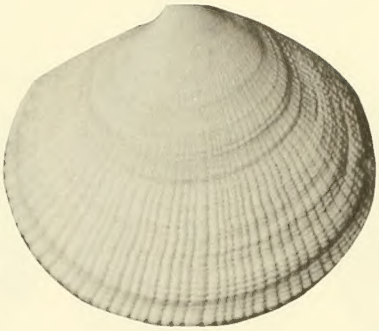
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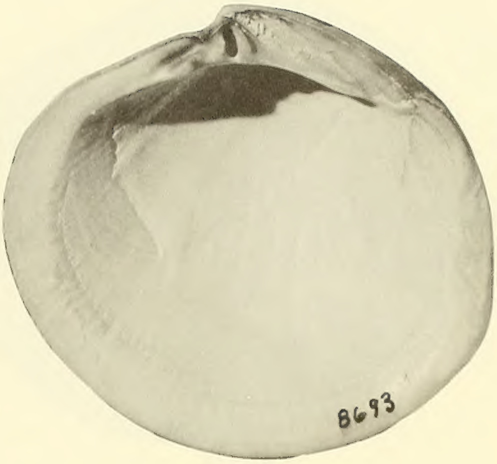

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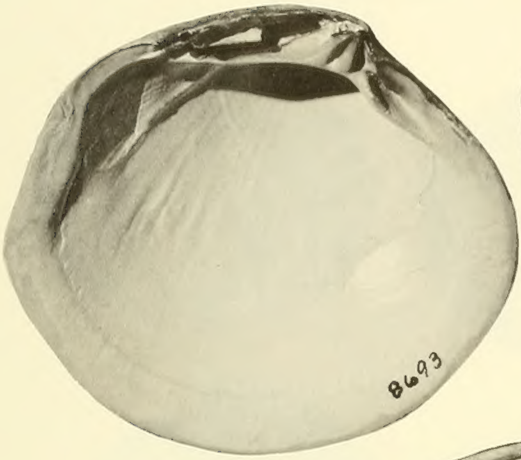

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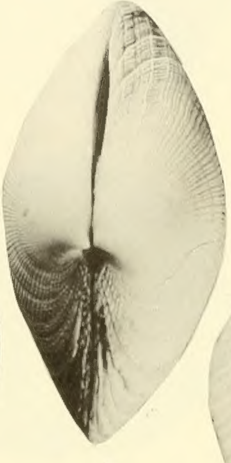
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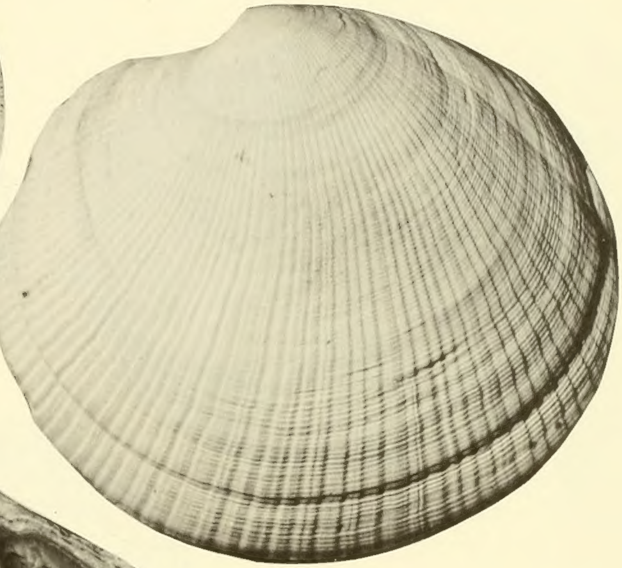
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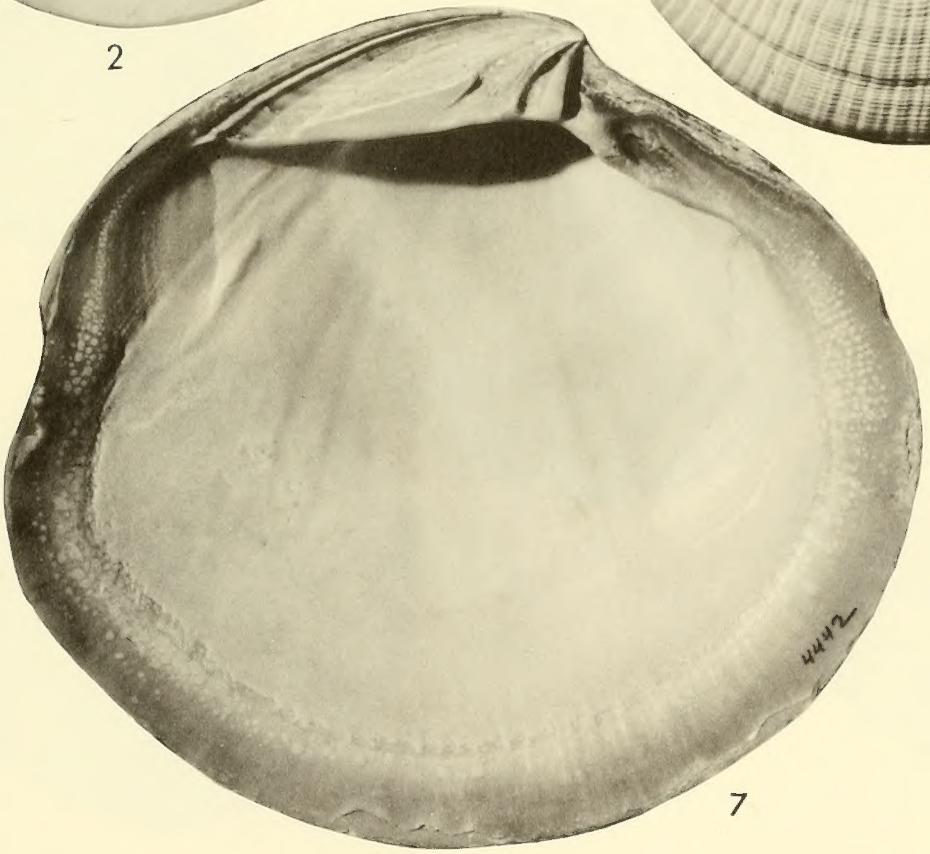

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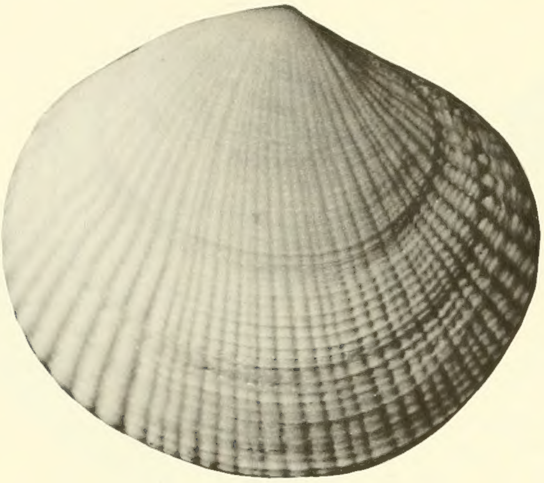
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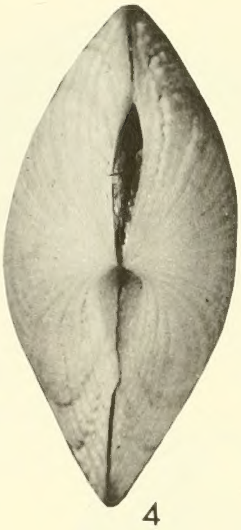
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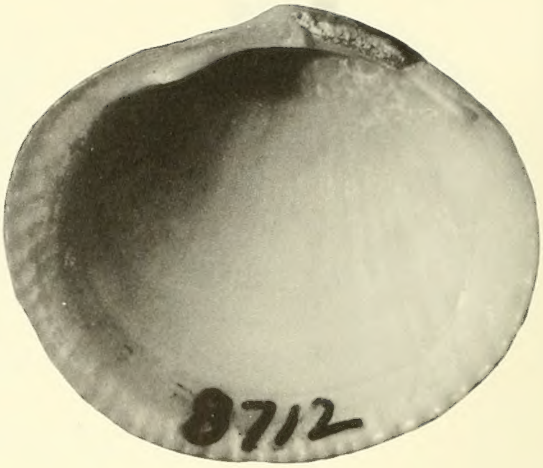

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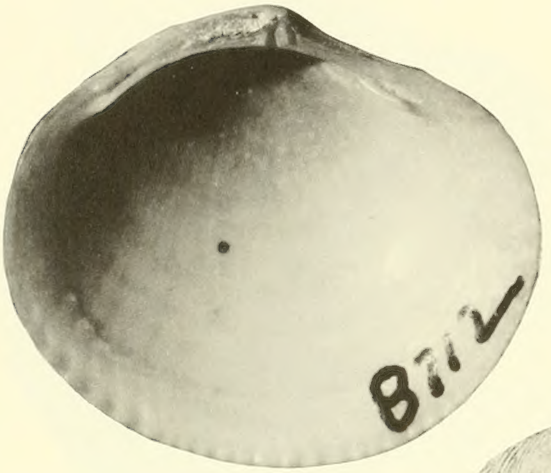

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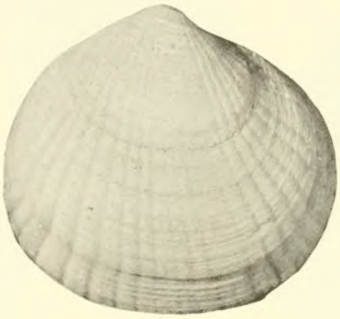
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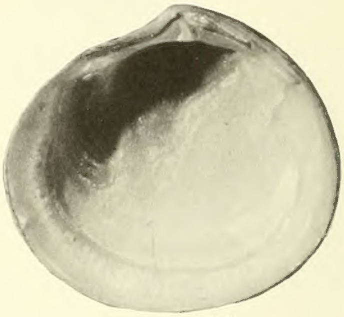
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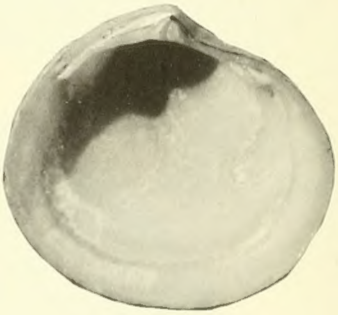
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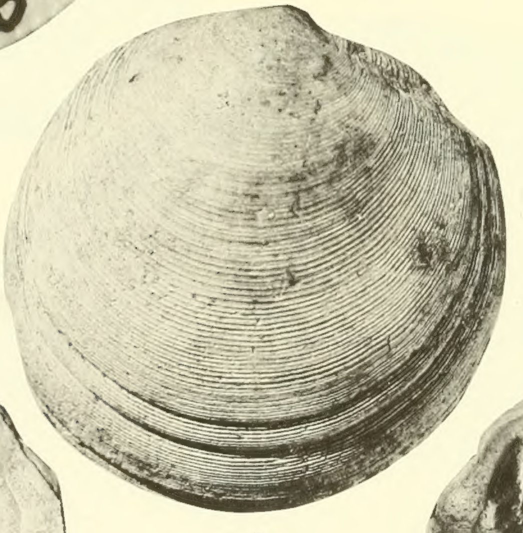
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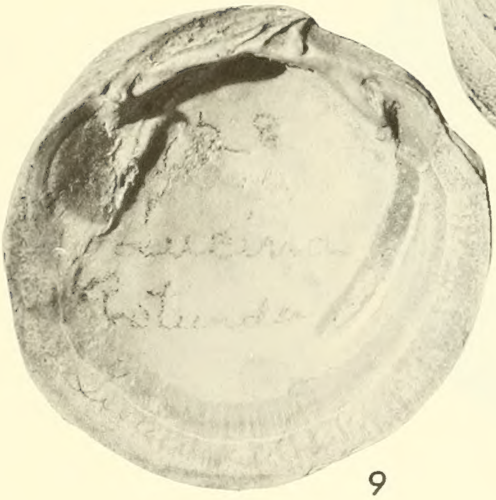
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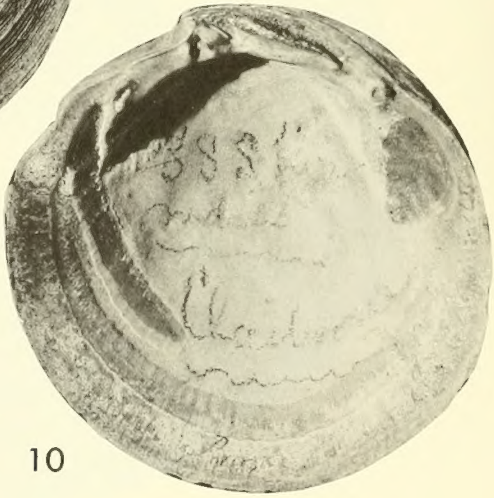
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## EXPLANATION OF PLATE 32

*Figure* *Page*

1-4. *Codakia (Ctena) mexicana* Dall ........ 285

1. Exterior of right valve. Recent, La Paz, Baja California. YPM-IZ 9082. (×4). 2. Interior of left valve of same specimen. 3. Interior of Fig. 1. 4. Top view of both valves, showing long, oval lunule.

5-7. *Codakia (Ctena) orbiculata* (Montagu) ........ 285

5. Exterior of right valve. Recent, Bermuda. YPM-IZ 9083. (×4). 6. Interior of Fig. 5. 7. Interior of left valve of same specimen.

8-10. *Codakia? (Claibornites) symmetrica* (Conrad) ........ 287

8. Exterior of right valve. Upper middle Eocene, Gosport Sand, Claiborne, Alabama. YPM-IP 27062. (×2). 9. Interior of left valve of same specimen. 10. Interior of Fig. 8.

## EXPLANATION OF PLATE 33

*Figure* *Page*

1-3. *Miltha (Miltha) xantusi* (Dall) .......... 289

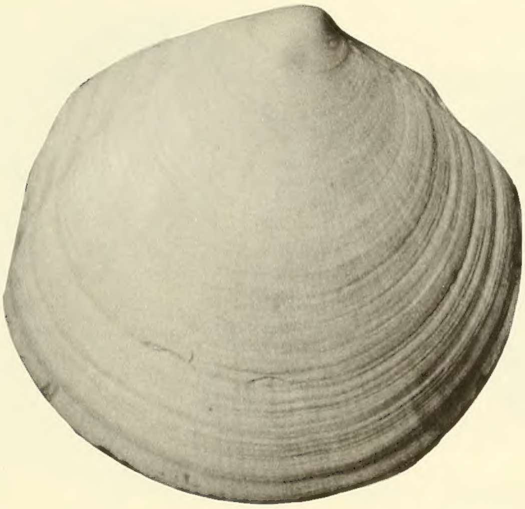
1. Exterior of right valve of one of two bivalved specimens, the syntypes of *Phacoides (Miltha) xantusi* Dall [see text]. Recent, Cape San Lucas, Baja California. USNM 5383a. (×1). 2. Interior of left valve of same specimen. 3. Interior of right valve of the second syntype of *P. (M.) xantusi* Dall; same locality. USNM 5383b. (×1).

4-7. *Miltha (Eomiltha) pandata* (Conrad) .......... 290

4. Exterior of right valve. Upper middle Eocene, Gosport Sand, Claiborne, Alabama. YPM-IP 27063. (×1). 5. Interior of left valve of same specimen. 6. Interior of Fig. 4. 7. Enlargement of hinge area of Fig. 6, showing bifid posterior cardinal. (×2).

8-10. *Miltha (Plastomiltha) claibornensis* (Conrad) .......... 292

8. Exterior of right valve. Upper middle Eocene, Gosport Sand, Claiborne, Alabama. USNM 90906. (×2). 9. Interior of fig. 8. 10. Interior of left valve. All but hinge area infilled by matrix; note impression on matrix of anterior adductor scar of corresponding right valve. Middle Eocene, Lisbon Formation, Lisbon Bluff, Alabama. USNM 154937. (×2).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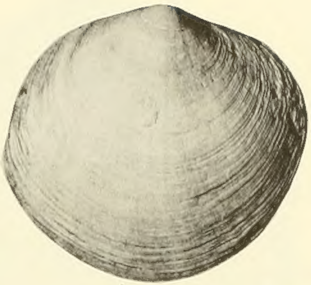
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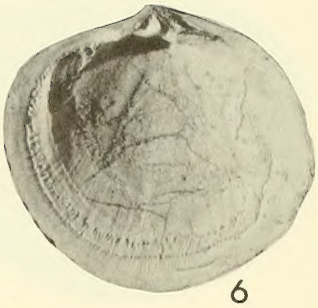
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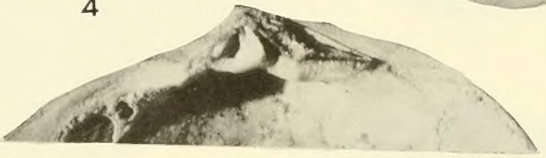
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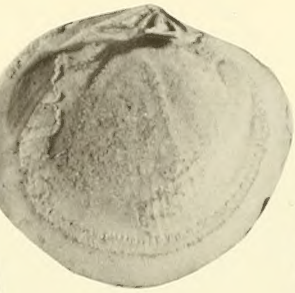
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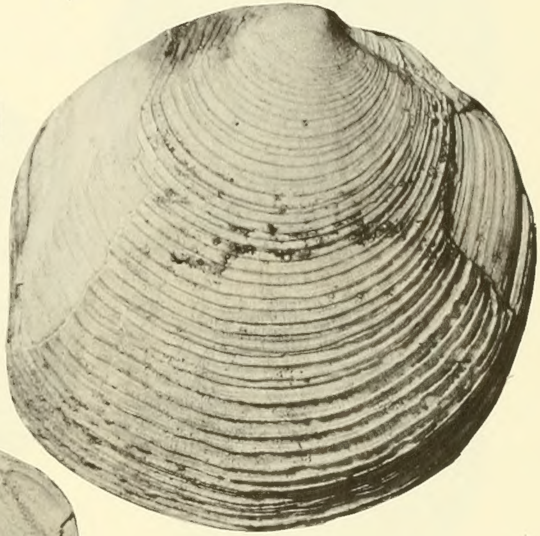
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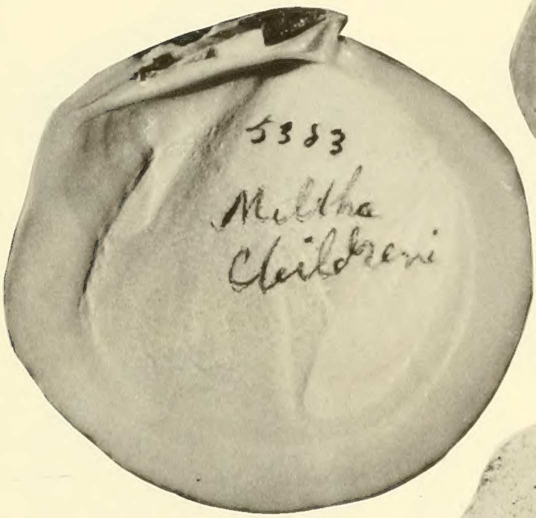

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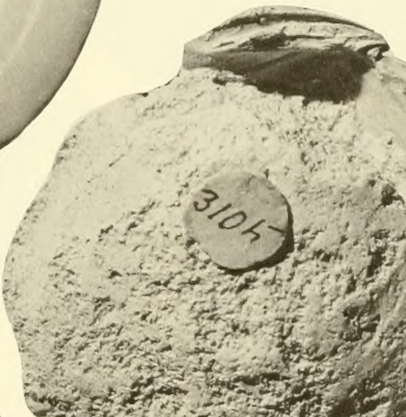

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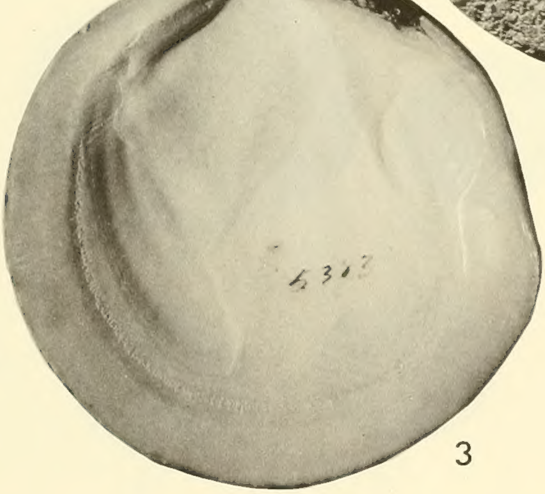

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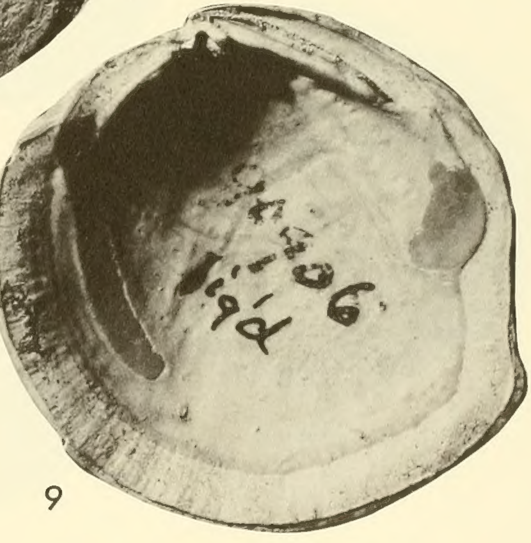
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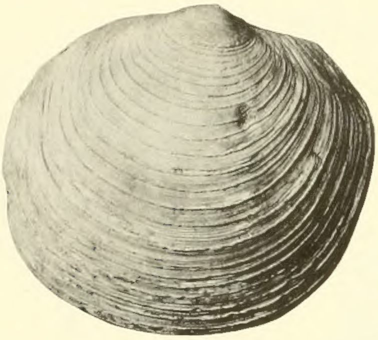
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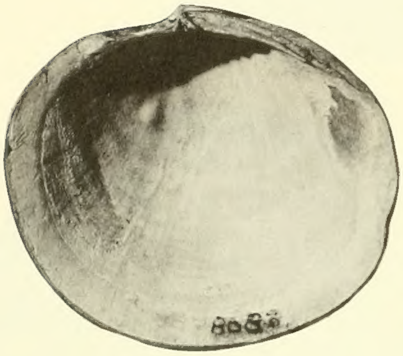
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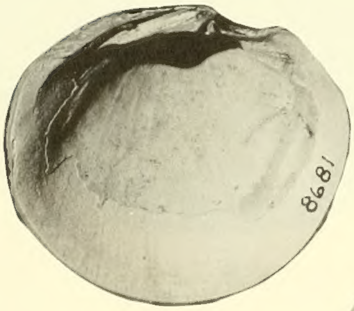
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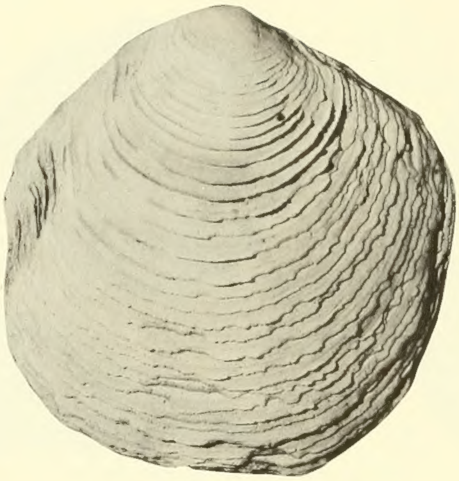
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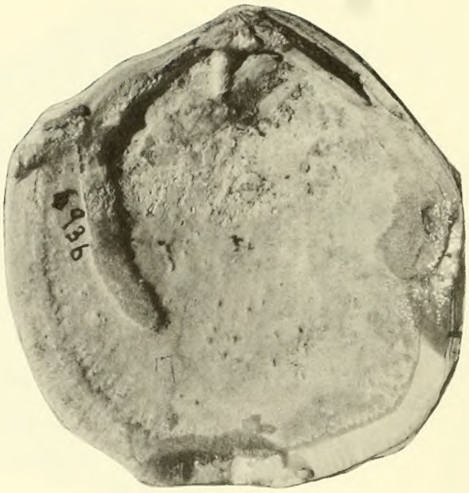
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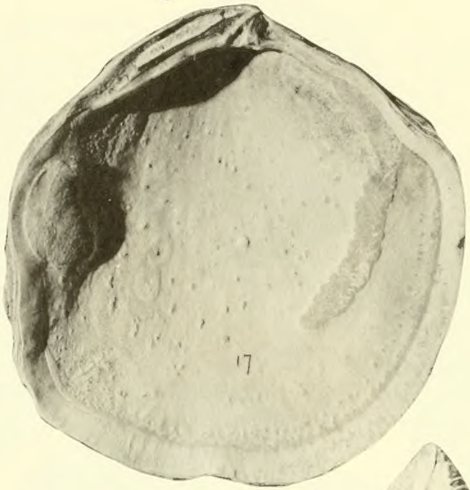
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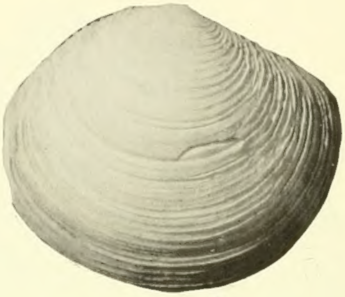
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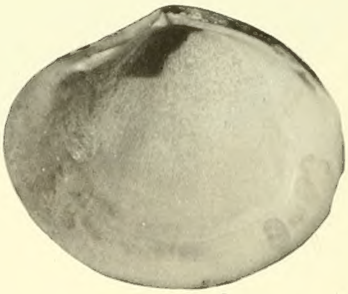
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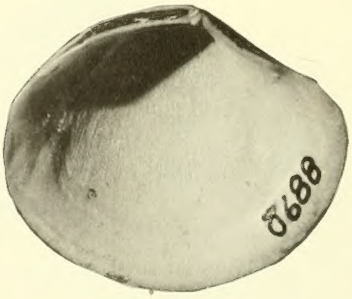
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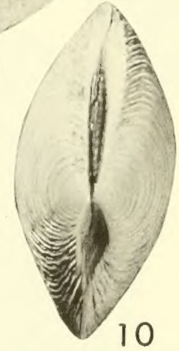
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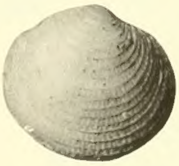
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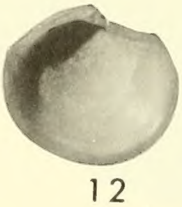
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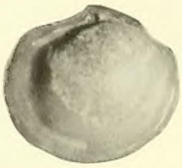
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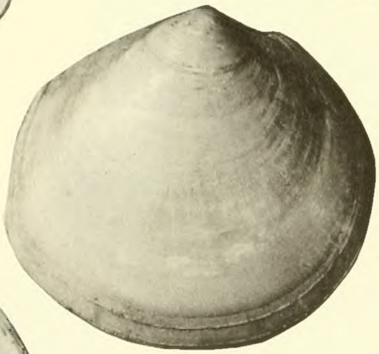
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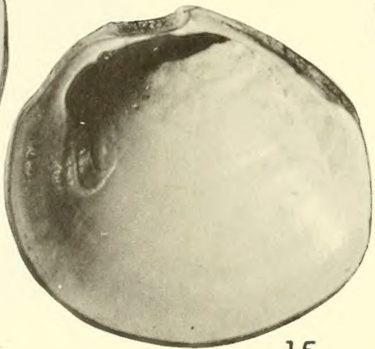
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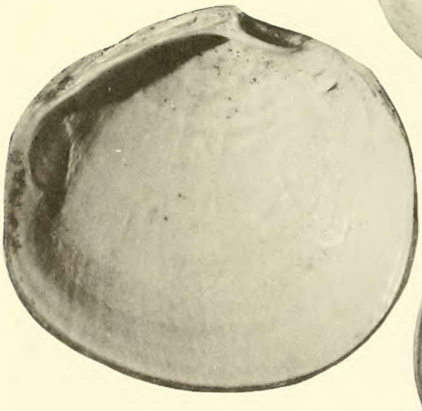
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## EXPLANATION OF PLATE 34

*Figure* *Page*

1-3. *Miltha (Lucinoma) filosa* (Stimpson) .......... 293

1. Exterior of right valve. Recent, U.S. Fish Commission Station 950, off Martha's Vineyard, Massachusetts. YPM-IZ 9084. (×1). 2. Interior of fig. 1, showing external, slightly inset ligament. 3. Interior of left valve from same locality, showing deeply inset ligament. YPM-IZ 9085. (×1.)

4-6. *Miltha (Armimiltha) disciformis* (Heilprin) .......... 294

4. Exterior of right valve. Pliocene, Caloosahatchee Formation, Caloosahatchee River, Florida. YPM-IP 6936. (×1). 5. Interior of fig. 4. 6. Interior of left valve of same specimen.

7-10. *Myrtea (Myrtea) spinifera* (Montagu) .......... 296

7. Exterior of right valve. Recent, England. YPM-IZ 9086. (×2). 8. Interior of fig. 7. 9. Interior of left valve of same specimen. 10. Top view of both valves in articulation, showing oval, asymmetrical lunule.

11-13. *Myrtea (Eulopia) sagrinata* (Dall) .......... 298

11. Exterior or right valve of holotype of *Lucina sagrinata* Dall. Recent, Gulf of Mexico. USNM 64277. (×4). 12. Interior of left valve of holotype. 13. Interior of right valve of holotype.

14-16. *Myrtea (Myrteopsis?) lens* (Verrill and Smith) .......... 299

14. Exterior of right valve. Recent, U.S. Fish Commission Station 876, off Martha's Vineyard, Mass. YPM-IZ 9087. (×4). 15. Interior of fig. 14. 16. Interior of left valve from same locality YPM-IZ 9088. (×4).

## EXPLANATION OF PLATE 35

*Figure* *Page*

1-3. *Myrtea? (Epilucina) californica* (Conrad) ........ 301

1. Exterior of left valve, showing strong posterior truncation. Recent, San Pedro Bay, California. YPM-IZ 9090. (×2). 2. Interior of left valve, showing rounded posterior margin. Recent, Point Loma, California. YPM-IZ 9089. (×2). 3. Interior of right valve of same specimen as Fig. 2.

4-6. *Anodontia (Anodontia) alba* Link ........ 303

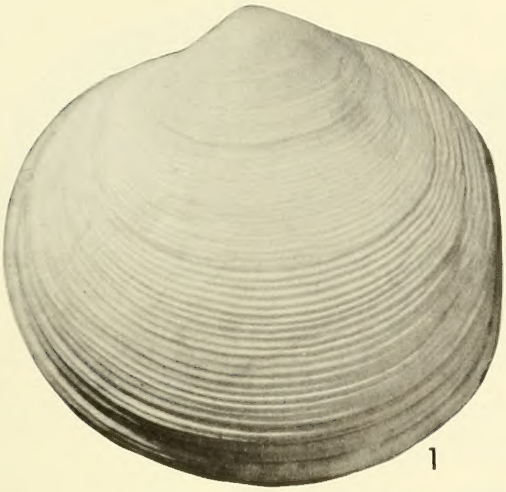
4. Exterior of right valve. Recent, Florida. YPM-IZ 9091. (×1). 5. Interior of Fig. 4. 6. Interior of left valve from same lot. YPM-IZ 9092. (×1).

7-10. *Anodontia (Anodontia) philippiana* (Reeve) ........ 304

7. Interior of right valve of small specimen, showing divergence of anterior adductor scar from pallial line (compare with Fig. 5). Recent, Sarasota, Florida. (×1). 8. Exterior of right valve of large specimen. Recent, Florida. YPM-IZ 9094. (×0.75). 9. Interior of left valve of same specimen. 10. Interior of Fig. 8.

11-13. *Anodontia (Eophysema) subvexa* (Conrad) ........ 305

11. Exterior of right valve of articulated specimen. Interior not known, but size corresponds to that of edentulous specimens called *Eophysema subvexa* by Palmer and Brann (1965) [see text]. Middle Eocene, Lisbon Formation, Claiborne, Alabama. USNM 129809. (×2). 12. Interior of right valve of small dentate specimen, corresponding in size and dentition to *Lucina subvexa* "var." *sylvaerupis* Harris, 1919 [see text]. Early? Eocene (horizon unrecorded), Woods Bluff, Alabama. USNM 129951a. (×4). 13. Interior of left valve of a second small dentate specimen from same locality. USNM 129951b. (×4).



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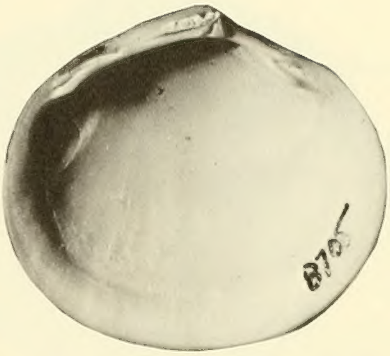

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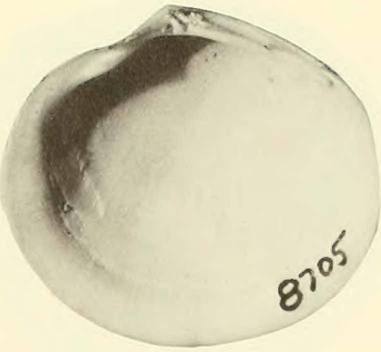

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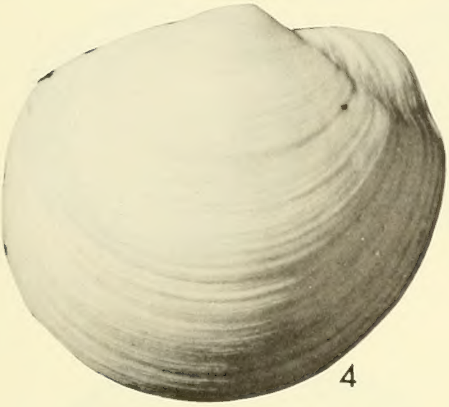

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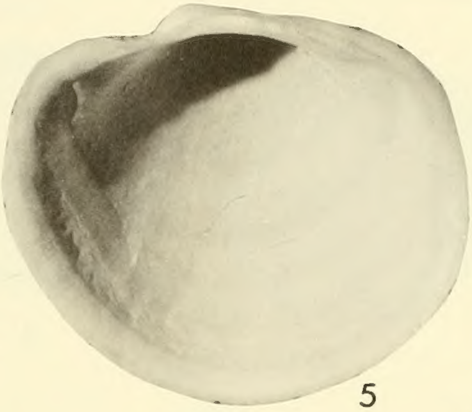

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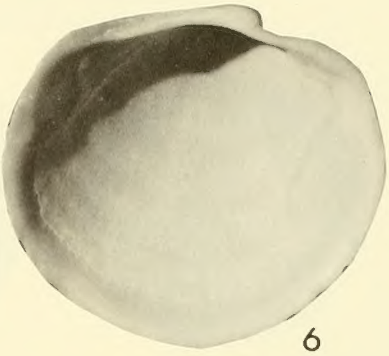

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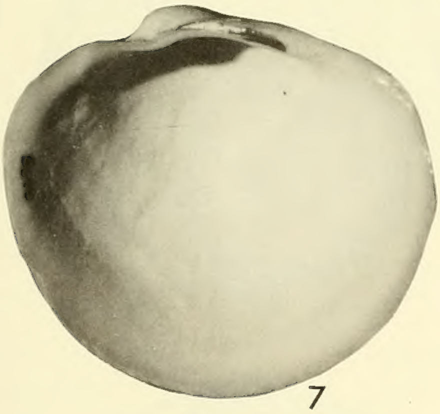

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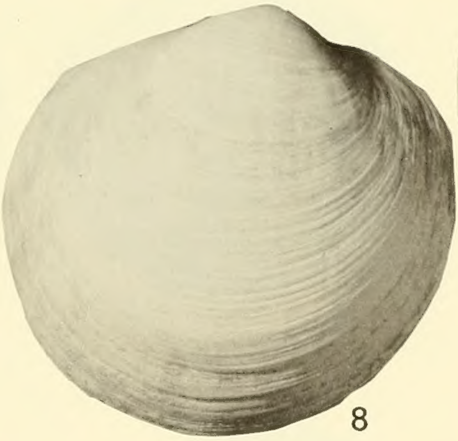

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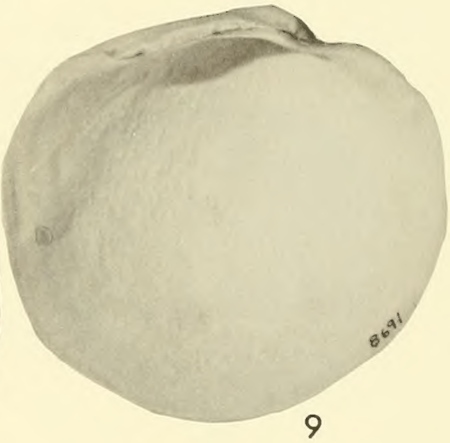

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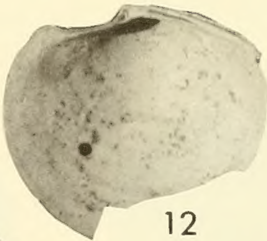

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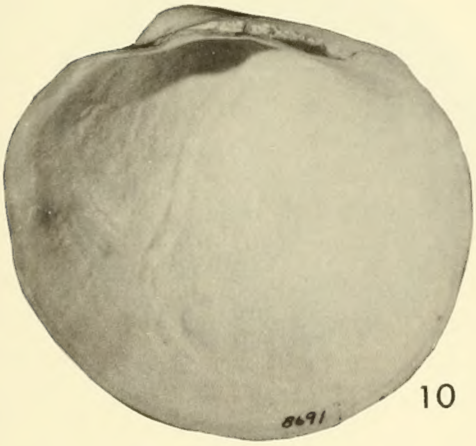

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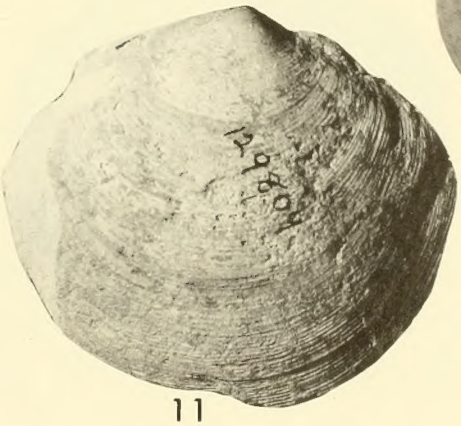

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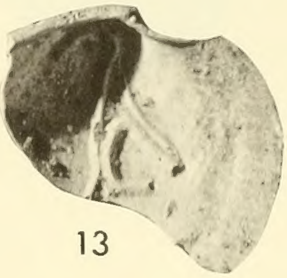

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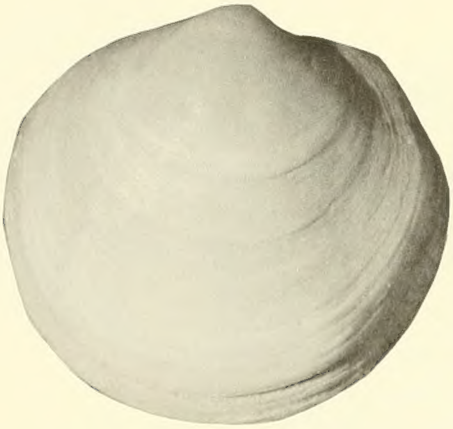
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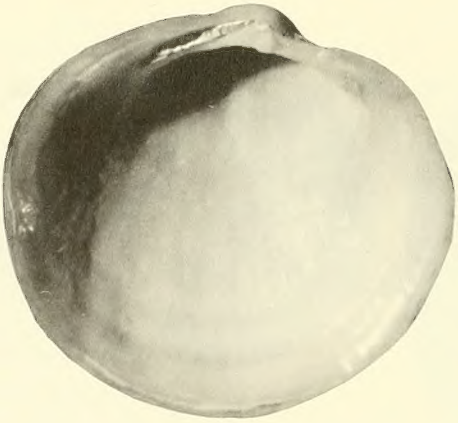
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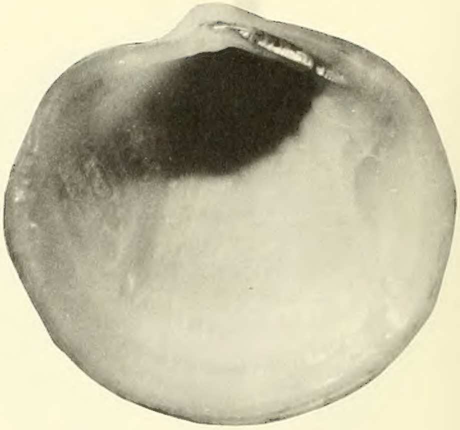
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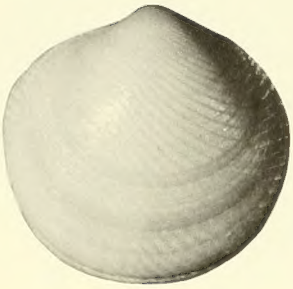
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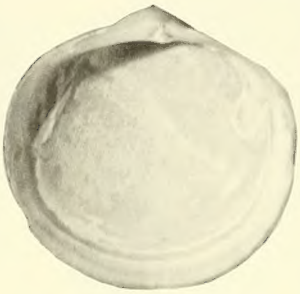
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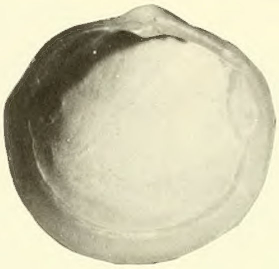
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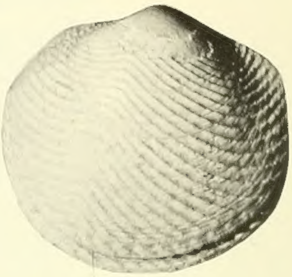
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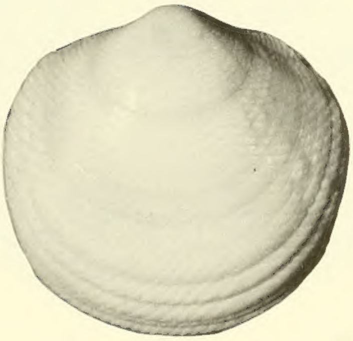
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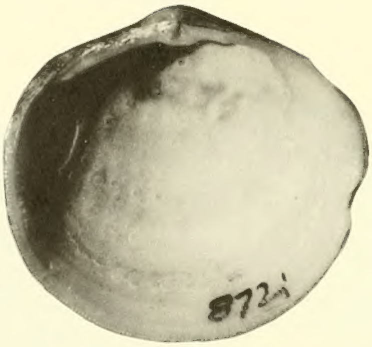

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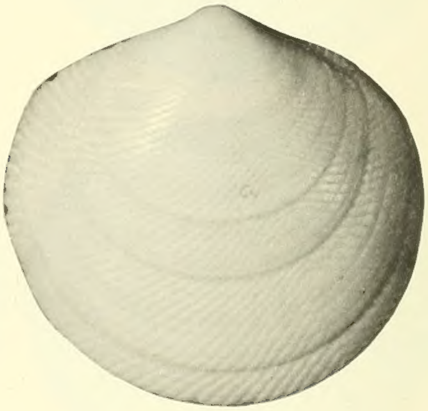
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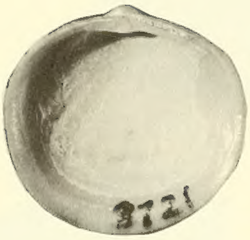

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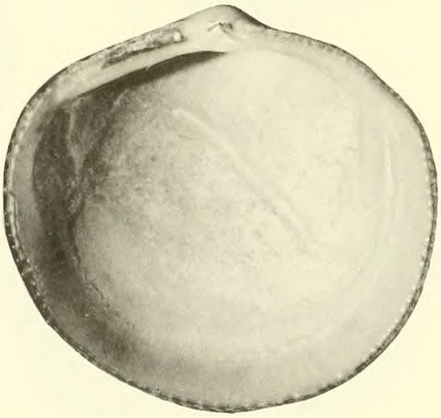
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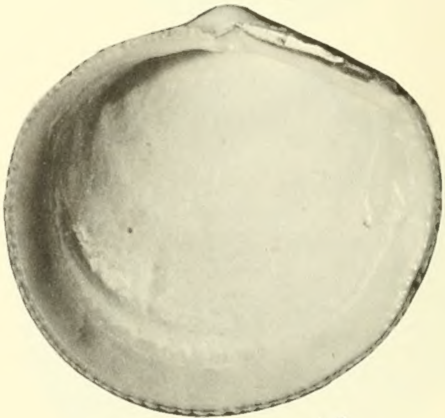
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## EXPLANATION OF PLATE 36

*Figure* *Page*

1-3. *Loripes (Loripes) lacteus* Poli ........ 308

1. Exterior of right valve. Recent, Syria. YPM-IZ 9095. (×4). 2. Interior of left valve of same specimen. 3. Interior of Fig. 1.

4-7. *Divaricella (Divalinga) quadrisulcata* (d'Orbigny) ........ 309

4. Exterior of left valve. Recent, White River Beach, Jamaica. YPM-IZ 9096. (×2). 5. Interior of Fig. 4. 6. Interior of right valve from same locality. YPM-IZ 9097. (×2). 7. Exterior of left valve. Cf. Fig. 4; note coarser sculpture and darker shell of this cold-water specimen. Recent, Buzzards Bay, off Quissett, Massachusetts. YPM-IP 27065. (×2).

8-10. *Divaricella (Divalinga) eburnea* (Reeve) ........ 310

8. Exterior of right valve. Recent, Cape San Lucas, Baja California. YPM-IZ 9098. (×2). 9. Interior of left valve from same locality. YPM-IZ 9099. (×2). 10. Interior of right valve from same locality. YPM-IZ 9100. (×2).

11-13. *Divaricella (Egracina) dentata* (Wood) ........ 311

11. Exterior of right valve. Recent, Florida. YPM-IZ 9101. (×2). 12. Interior of left valve of same specimen. 13. Interior of Fig. 11.

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VOL. VIII

No. 51

# MORPHOLOGY AND ANATOMY OF ANEUROPHYTON, A PROGYMNOSPERM FROM THE LATE DEVONIAN OF NEW YORK

By

BRUCE S. SERLIN AND HARLAN P. BANKS

1978

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Paleontological Research Institution
Ithaca, New York, U.S.A. 14850

*Library of Congress Card Number: 78-59640*

Printed in the United States of America
Arnold Printing Corporation
Ithaca, New York 14850

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# MORPHOLOGY AND ANATOMY OF *ANEUROPHYTON*, A PROGYMNOSPERM FROM THE LATE DEVONIAN OF NEW YORK

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## ABSTRACT

*Aneurophyton germanicum* was collected in rocks of Frasnian (Late Devonian) age in southeastern New York. The plants grew on a coastal plain (formerly the "Catskill Delta") on the margin of the Devonian inland sea. The sterile branch system consists of three orders of branching with ultimate appendages borne on the third order. All branching is spiral. Ultimate appendages dichotomize one to three times and are three-dimensional when more than once divided. Fertile systems are also branched spirally. Fructifications are stalked, lyre-shaped, 10 mm in length, and bear sporangia on the two arms. Sporangia appear to be inserted in two rows. Each sporangium is 2.0 mm long and oblong-elliptical in outline. The protostele is triangular in transverse section with slightly concave sides. Primary xylem is mesarch with one protoxylem strand near the apex of each lobe and one central. Secondary xylem is composed of tracheids and high, uniseriate rays. *Aneurophyton* appears to be the simplest member of Aneurophytales on the basis of both anatomy and morphology. This is the first report of *A. germanicum,* and perhaps the first valid report of the genus, in North America. It extends the range of the species from Middle into Upper Devonian strata.

## ACKNOWLEDGMENTS

This research was supported by Federal Hatch Funds, administered by the Director of Research, New York State College of Agriculture and Life Sciences. It was part of a thesis submitted to Cornell University in partial fulfillment of the degree of M.Sc.

We thank Brenda Colthart for her skill in the production of the photographs.

The senior author thanks Dr. Bruce Bell for the opportunity to examine the Goldring collection of *Eospermatopteris* at the New York State Museum, Albany, New York.

## INTRODUCTION

*Aneurophyton germanicum* has come to be recognized as a typical component of Eifelian and Givetian floras of Europe and the Soviet Union. It has also been accepted as representative of primitive progymnosperms. Nevertheless it has no holotype, the original collections of Kräusel and Weyland were destroyed, the morphology of its fructification is little understood, and its anatomy is poorly known. Further, it has recently (Mustafa, 1975) been placed in synonymy with *Rellimia (Protopteridium)* Leclerq and Bonamo (1973). Thus it seems significant to report on material from New York State that clarifies the structure of the fructification and includes anatomy taken from an axis identifiable as *A. germanicum.* We begin with a brief survey of earlier pertinent work in New York.

Dawson (1871) described two new species of fossil tree ferns from New York State solely on the basis of short lengths of trunks which he thought were covered by aerial roots. *Psaronius erianus* was invested by parallel roots, *P. textilis* by roots that anastomosed. Goldring (1924) found many similar stumps *in situ* at Gilboa, New York, during quarrying operations associated with the building of a dam on the Schoharie River. Associated with the stumps, but never in organic connection, she found isolated seeds, microsporangia, and tripinnate fronds up to six feet long bearing twice bilobed, recurved ultimate appendages. Impressed by the possibility that all these isolated organs comprised a single plant, she described the genus *Eospermatopteris* and renamed Dawson's two species *E. eriana* and *E. textilis.* She regarded the aerial roots described by Dawson as sclerenchymatous cortex like that found in seed ferns. This and the mega- and microsporangia convinced her that she had found a forest of pteridosperms which she referred to as Dawn Seed Ferns.

Kräusel and Weyland (1923) named the genus *Aneurophyton* for fernlike foliage that was two or three times pinnate, bearing bilobed, recurved ultimate appendages. Fertile fronds were less branched but otherwise comparable to the sterile. Sporangia were stalked and oblong-elliptic. Vascular strands were present in all parts except the ultimate appendages, and included secondary xylem. In 1926 and 1929 Kräusel and Weyland added to the original description such features as variability in the form of fertile pinnules, the presence of a triangular protostele with three mesarch protoxylem strands, and repetition of the anatomical pattern in all orders of branching except the ultimate appendages. The last two characteristics led them to suggest that the frond of *Aneurophyton* was not a typical frond (now called a branch system) and that it might be three-dimensional rather than a planated structure.

Six years later Kräusel and Weyland (1935) reported that the cortical pattern observed on trunks of *Eospermatopteris eriana* represented outer cortex and that the pattern seen on *E. textilis* could be found deeper in the cortex of a single specimen of *E. eriana.* They found this to be true of specimens from both Germany and New York. They concluded that only one species existed and suggested it be named *E. textilis.* We suggest *E. eriana* be used because it appears before *E. textilis in* Dawson (1871) and, therefore, has priority. Kräusel and Weyland (1935) macerated some of Goldring's isolated "seeds" and found that they contained spores. The microsporangia they dismissed as inorganic markings. That left the foliage of Goldring as sterile branch systems which they considered sufficiently similar to their German collections to be renamed *Aneurophyton textile* (or, as we suggest because of priority, *A. erianum*). Thus by 1935, *A. erianum* (Goldring), Kr. and W., 1935, and *E.*

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*eriana* Goldring, 1924, were recognized in New York and *A. germanicum* Kr. and W., 1923, and *E. germanica* Kr. and W., 1935, in Germany.

Leclercq (1940) assigned several specimens to *Aneurophyton* based primarily on a branch which had a triangular primary xylem. She reported a fourth protoxylem strand to be present in the center of the protostele.

Arnold (1940) described *Aneurophyton hallii* (Dawson), Arnold, on the basis of permineralized branches from western New York that had triangular protosteles and secondary xylem. Scheckler and Banks (1971a) transferred Arnold's specimens to *Triloboxylon* because reexamination of the slides showed not three, or four, but many protoxylem strands in the primary xylem.

Stockmans (1948) described a new species of *Aneurophyton, A. olnense,* from Belgium. It was more robust than *A. germanicum* and occurred in Upper rather than Middle Devonian strata.

There are two other questionable species of *Aneurophyton*. Termier and Termier (1950) described *A. maroccanum* for sterile specimens from the Eifelian of central Morocco. Stockmans (1968) described *A.* (?) *furcatum* from strata close to the Givetian-Frasnian boundary in Belgium.

## LOCALITY AND STRATIGRAPHY

Our material was collected by Banks at a now abandoned roadside quarry close to the edge of the Delaware River. The quarry lies one mile (1.6 km) southeast of Pond Eddy on New York State Route 97 which parallels the River. Fish Cabin Creek feeds into the Delaware at this point and the Creek can be located on Milford, Pa.-N.Y.-N.J. 15′ Quadrangle Map, 1915. The bulk of the collection was made in 1938 during road-building operations. Additional specimens have been obtained in subsequent years. This quarry is the source of the lycopod *Colpodexylon deatsii* Banks, 1944, *Eddya sullivanensis* Beck, 1967, and fragments of cf. *Eospermatopteris* (unpublished).

The plants are found in a fine-grained siltstone, a member of the Delaware River Formation (Fletcher and Woodrow, 1970). This formation at Pond Eddy is a non-marine correlative of the lowermost Walton Formation and much of the underlying Oneonta Formation. The younger part of the Delaware River Formation belongs to the Sonyea Group, the older to the Genesee Group (Rickard, 1975). It thus belongs to the Finger Lakes Stage, Senecan Series (= Frasnian of Europe) of the Upper Devonian System. Paleocurrents indicate that the source of the sediment lay to the southeast of Milford, Pennsylvania, some 17.6 km away from Pond Eddy (Fletcher and Woodrow, 1970). The Delaware River Formation appears to have been deposited by a fluvial system close to the shore-line along a low plain (Allen, 1965; Fletcher and Woodrow, 1967). The water table in the area of deposition was apparently "sufficiently high to prevent oxidation of the muds" (Fletcher and Woodrow, 1970). This reducing condition created a suitable environment for preservation of an abundance of plant remains.

In addition to the specimens from New York we had available a small collection of *Aneurophyton germanicum* identified by Dr. H. Weyland. It was obtained some years ago from Dr. F. Krantz of Bonn, Germany. It was collected in the Middle Devonian Honseler beds (Givetian) at Kirberg near Elberfeld in the Rhineland, Germany, possibly from the same locality that yielded the type specimens.

## METHODS

The fossils are found almost exclusively as compressions. Short segments of axes show cellular preservation by iron pyrite. The technique called dégagement by Leclercq (1960) proved to be the most effective means of following axes into the matrix or into a counterpart. Commercially produced needles (John English Glovers needles) with triangular points are useful in delicate areas. Needles fashioned out of tungsten wire are also valuable.

Hard needles are produced by heating tungsten wire white hot in the flame of an oxygen torch and then placing the wire in a heated solution of sodium nitrite. Flexible needles are made by placing a wire into sodium nitrite solution, withdrawing it, and repeating the process several times to build up a coating of sodium nitrite crystals on the wire. Once coated the wire is set on a hot plate. The wire becomes red and the crystals begin to melt. At this stage the wire is held at an angle and rolled on the surface of the hot plate. This causes the wire to be uniformly oxidized and a sharp tip is obtained.

Some specimens have been treated by the transfer technique (Bonamo and Banks, 1967) and others by the interrupted transfer technique (Banks, Bonamo, and Grierson, 1972). Clearing techniques designed to reveal epidermal patterns were unsuccessful, perhaps because the specimens appear to have undergone some degree of metamorphism.

Anatomically preserved material was coated with Bioplastic (Ward's Natural Science Establishment, Inc., Rochester, N.Y.) without the hardening agent and placed in a vacuum chamber to draw air out of cracks. It was then transferred to catalyzed Bioplastic, hardened one day at room temperature, and then cured in an oven at 60° C overnight. Serial sections were cut on a Gillings-Hamco dental saw. Following grinding and polishing, sections were etched 5-15 seconds in $HNO_3$ (Scheckler and Banks, 1971a), washed in water, neutralized in sodium bicarbonate, dried, and then mounted on slides in Harleco Synthetic Resin dissolved in xylene. Longitudinal sections were made by splitting pyrite or by cutting and grinding thin sections.

Photomicrographs were made with a Bausch and Lomb metallurgical microscope; macrophotographs with a Nikon 35 mm camera and a Leitz Aristophot.

## DESCRIPTION

### STERILE BRANCH SYSTEM

The most complete specimen of sterile branch system is 115 mm long (Pl. 37, fig. 1). It is incomplete at both ends but tapers in diameter distally from 5 to 4 mm. It bears branches at intervals of 11 to 15 mm. When the specimen was split for the first time, branches B, C, and G (Pl. 37, fig. 1) were the only ones that were obviously attached. Dégagement revealed the attachment of seven more. The branches arise in a spiral sequence. Branch A (Pl. 37, fig. 1, arrow indicates position of its attachment) is attached to the upper surface of the main axis and extends into the counterpart. Branch B extends downward into the matrix from the lower side of the main axis. Further out it bends upward so that it can be seen on the counterpart (Pl. 37, fig. 2). Branch C is attached just below the plane in which the main axis lies. Branch D (Pl. 37, fig. 1, line indicates position of attachment) is attached to the upper surface of the main axis and extends into the counterpart. It is illustrated (Pl. 37, fig. 2, arrow) near the edge of the counterpart in attachment to a piece of the main axis (ax) that was lifted when the counterpart was removed. The remaining branches, E - J (Pl. 37, fig. 1), similarly are attached to various levels of the main axis and thus demonstrate spiral arrangement.

Branch F is the most complete and provides the best indication of lesser orders of branching. It bears two laterals (Pl. 37, fig. 3, arrows 1 and 2). The more proximal (1) bears two laterals (ultimates, u) that terminate in bilobed apices. The more distal (2) bears only the bases of two laterals (ultimates).

The specimen in Plate 37, figure 1 thus demonstrates four orders of branching. It is not known to what the main axis was attached. This axis is, therefore, arbitrarily designated n + 1. The branches it bears are called n + 2. They in turn bear penultimate branches from which bilobed ultimate appendages, the fourth order, arise.

A second specimen (Pl. 37, fig. 4) illustrates certain features of n + 2 and lesser orders of branching. This specimen at the outset seemed to be only an axis with five laterals (penultimates 1, 2, 3, 4, 6) attached. Dégagement soon uncovered a sixth penultimate and then bilobed ultimate appendages (arrows). Dégagement also reveals that the branching at the base of the n + 2 is a dichotomy (Pl. 37, fig. 4, arrow d) and that the right arm of the dichotomy also bears both penultimates (arrow p) and ultimates. Spiral arrangement characterizes penultimates just as it does n + 2 branches. Branches 1, 3, and 5 extend at various angles down into the matrix. Branches 2 and 4 extend horizontally in more or less the same plane as the n + 2 but at different angles from one another. Branch 6 is attached to the upper side of the n + 2 and extends upward from it. Penultimate branches are 1.5 - 2.0 mm in diameter and up to 54 mm in length. They are often spaced at intervals of 8.0 mm. Some penultimates terminate in a bilobed structure similar to an ultimate appendage and some bifurcate like n + 2 axes (Pl. 37, fig. 5).

Ultimate appendages are usually embedded and can be followed into the matrix only by careful uncovering with needles. This suggests that they have retained their original spiral arrangement. They are usually bilobed structures (Pl. 37, fig. 7). The main stalk of the appendage varies from 4.0-7.0 mm in length and is 1.2 mm in diameter. The tips of the arms of the dichotomy spread from 4.0-7.0 mm apart and usually end in rounded tips (Pl. 37, fig. 7). Some end in pointed tips (Pl. 38, fig. 9). Arms usually recurve away from each other (Pl. 37, fig. 7). Variations include arms spread in an almost horizontal plane (Pl. 38, fig. 9) and arms that originate typically but then are reflexed back toward the opposite arm.

Occasionally one arm of the dichotomy of an ultimate appendage divides a second time resulting in three tips (Pl. 37, fig. 6; Pl. 38, fig. 8). Four such appendages are illustrated on Plate 37, figure 5, the first, second, and fourth on the left arm of the dichotomy and the first on the right arm of the dichotomy. Invariably the unbranched arm of the first dichotomy bends abruptly upward or downward. The arms of the second dichotomy remain in a horizontal plane. The evidence suggests strongly that the resulting ultimate appendage is not flattened in one plane, or planated, but rather that it is a three-dimensional structure.

Ultimate appendages, like larger orders of branching, are borne spirally. One penultimate branch bears four appendages (Pl. 38, fig. 10, arrows 1-4). Branch 1 extends directly upward into the matrix from the penultimate. Branch 2 extends gently downward from the penultimate. Branch 3 extends obliquely upward from the penultimate on the opposite side from branch 2. The fourth extends upward into the matrix from the penultimate. This spiral arrangement is made even clearer when one studies both part and counterpart of the specimen because fragments of each appendage are present on both. Spacing between ultimates varies from 3.5-5.5 mm.

### FERTILE BRANCH SYSTEM

Reproductive systems (Pl. 38, fig. 11) are represented by three orders of branching only: n + 2, penultimate, and ultimate (the fructification). The longest n + 2 branch measures 60 mm and is 2.0 mm in diameter. Penultimate appendages are 25 mm or more in length and 1.0-1.5 mm in diameter. They are arranged spirally. Three penultimate branches (Pl. 38, fig. 11, Nos. 1, 2, 3) are distinctly attached to the n + 2 axis. Two of them (1, 2) are bent proximally. The third (3) is oriented more normally and extends in a distal direction. A fourth penultimate (Pl. 38, fig. 11, No. 4) arises from the upper side of the n + 2 which then plunges into the matrix. Hence the fourth penultimate simulates a continuation of the n + 2. The n + 2 axis (Pl. 38, fig. 11) is further complicated by the fact that its proximal third extends down into the matrix and had to be uncovered to a depth of at least 7.0 mm in order to demonstrate the attachment of penultimate No. 1. The four penultimate branches demonstrate spiral arrangement as branch 1 rises almost vertically from the left side of the n + 2. Branch 2 rises upward from the right side of the n + 2, branch 3 extends downward into the matrix and branch 4 extends upward from the surface of the n + 2. Penultimate branches also dichotomize (Pl. 38, fig. 11, arrow d).

Fructifications (Pl. 38, figs. 11, 12, 13) seen in lateral view consist of a central stalk (Pl. 38, figs. 13, S) that is 5.0-6.0 mm long and 1.0-1.5 mm in diameter. It dichotomizes once into two equal arms that recurve toward one another, terminate in blunt tips, and form a lyre-shaped structure. Plate 39, figure 15 shows another typical fructification that was uncovered to reveal details of sporangia. One arm of the lyre (Pl. 39, fig. 15) is intact and bears numerous sporangia. All but the base of the other arm is missing. Short stalks, 0.5 long by 0.5 mm in diameter arise from the inner margins of the arms of the lyre. Each stalk is terminated by a single sporangium (Pl. 39, fig. 19, st). The sporangia appear to be borne in a staggered, two-rowed arrangement (Pl. 39, figs. 15, arrows 1, 2; 19); Sporangia average 2.0 mm in length, ranging from 1.2-2.5 mm. They are 0.5 mm in diameter, oblong-elliptical in outline, and have rounded apices. As many as 18 sporangia have been found in one fructification.

Fructifications are also preserved as if flattened and viewed from above. Such an appearance is seen in Plate 38, figure 12, arrow a. In this view the attachment of the fructification and its stalk are hidden. Gradual removal of sporangia and arms of the fructification reveals its stalk (Pl. 38, fig. 13, $S_1$) and its attachment to penultimate No. 3 (cf. Pl. 38, fig. 11). The penultimate bends to the right beyond the attachment of the stalk. Complete removal of fructification a on Plate 38, figure 12 also clarified the position of the more proximal fructification b (Pl. 38, fig. 13) that is attached to the same penultimate.

Some fructifications seem distinctly different and for that reason are referred to as atypical (Pl. 39, figs. 16, 19). Their central stalk is only 2.0-3.0 mm long, only half the typical length. The stalk appears to have dichotomized to produce two arms each about 6.0 mm long and 1.0 mm in diameter. However, the two arms recurve toward the penultimate branch, the reverse of the direction in the typical lyre-shaped fructifications. Stalks arising from the concave side of the arms terminate in sporangia just as in the typical fructification. The use of the term atypical results from both the reflexed position of the arms and the apparent attachment of sporangia on their lower rather than upper surface. An explanation for this apparent abnormality is suggested in the discussion.

The amount of uncovering required to see the atypical fructification as shown in Plate 39, figure 19 is illustrated in Plate 39, figures 17-19. Plate 39, figure 17 (arrow) is a low magnification of the original appearance of the fructification. Plate 39, figure 18, at a higher magnification, shows the stalk (S) and the arms of the fructification (b,c) beyond its dichotomy. Little evidence of sporangia is seen. As dégagement proceeded, sporangia appeared and it was necessary to remove much of the stalk of the fructification in order to uncover sporangia. At the termination of the process, the distal portion of the stalk (Pl. 39, fig. 19, arrow S), the two arms of the fructification and numerous intact sporangia are revealed. The sporangium (Pl. 39, fig. 19) on which the letters st rest and the adjacent sporangium that is indicated by the head of the arrow suggest that here, as in typical fructifications, sporangia are borne in two rows. The morphology of fructifications illustrated in Plate 39, figures 15 and 16 was also clarified by dégagement.

The most significant feature revealed by the uncovering of fructifications, both typical and atypical, is that stalked sporangia are borne directly on the lyre-shaped arms. No lateral branchlets of any kind were found as uncovering proceeded from a stage like that shown in Plate 39, figure 18 to that in Plate 39, figure 19. In an effort to be certain that no branchlets had been missed, the specimens shown in Plate 39, figures 19 and 15 were subjected to continued dégagement so that now nothing remains of them. Still no lateral branchlets were found and the attachment of sporangia only to the arms of the lyre-shaped fructification seems a certainty.

Plate 38, figure 14 illustrates a lyre-shaped fructification from *Aneurophyton germanicum* identified by Weyland. It was collected from what we believe to be the same locality as the type material of the species. It suggests to us that there is little difference between our material and that of Kräusel and Weyland.

## ANATOMY

A structurally preserved axis in our material has proved to have the characteristics of *Aneurophyton.* The axis, an n + 2, bears three penultimate branches (Pl. 40, fig. 20, arrows 1, 2, 3). The counterpart of the specimen (Pl. 40, fig. 21) bears part of the n + 2 and also penultimates 1 and 3. Penultimate 1 is much more complete on the counterpart. It extends obliquely through the matrix and bears an ultimate appendage on the opposite side to that figured in Plate 40, figure 21. The pyritized section from which slides were made lay between the $\Delta$'s on the n + 2 (Pl. 40, fig. 20).

The primary xylem is triangular in transverse section. The sides of the triangle are slightly concave, the apices rounded (Pl. 40, fig. 22). Four protoxylem strands are present between branchings. One is central, three occur near the apices of the lobes (Pl. 40, fig. 22, arrows). Thus protoxylem is mesarch.

A series of sections suggests the manner of formation and departure of the vascular supply to a penultimate branch. Below the origin of a branch a lobe of primary xylem has a single protoxylem strand (Pl. 40, fig. 23). At a higher level both the lobe and the strand are elongated radially (Pl. 40, fig. 24). Still higher up the protoxylem has divided and two strands are found along one radius. One of these remains in the parent lobe, the other supplies the branch trace. During the division of the protoxylem strand, the apex of the lobe elongates radially. Higher up a branch trace appears (Pl. 40, fig. 25, arrows). It has, at this stage, two or possibly three protoxylem strands (Pl. 41, figs. 26, 27, arrows). Preservation of the trace is such that the study of a series of sections is required to demonstrate that its shape is essentially triangular. In Plate 41, figures 26 and 27 the base of the triangle is still attached to the parent lobe and a portion of its apex is unpreserved. Hence a cursory examination might suggest that its shape is elliptical.

Primary xylem is composed exclusively of tracheary elements. Development of secondary xylem commences along the concave sides of the primary xylem (Pl. 40, fig. 22). Tracheids and vascular rays characterise the secondary xylem (Pl. 41, figs. 28, 29). Radial walls of tracheids are covered by 1-5 rows of elliptical bordered pits (Pl. 41, fig. 30). All rays observed were uniseriate and from 2-27 cells in height (Pl. 41, fig. 29). Ray cells are procumbent and relatively thin-walled (Pl. 41, fig. 28).

## DIAGNOSIS

### Genus **ANEUROPHYTON** Kräusel & Weyland, 1923

*Generic diagnosis.* — Emended Kräusel and Weyland, 1929; here emended and amplified. Three orders of branching and ultimate appendages known for sterile material, two orders and fructifications for fertile. All branches spirally arranged. Ultimate appendages 1-3 times dichotomized, unwebbed and probably three-dimensional when more than once forked. Fructifications lyre-shaped; stalked sporangia oblong-elliptic in outline, inserted in two rows on each arm of fructification. Primary xylem of all orders of branching except ultimates three-lobed with four mesarch protoxylem strands, one near the tip of each lobe and one central. Secondary xylem of tracheids and rays. Anatomy of ultimate appendages and fructifications unknown.

*Type of the genus.* — *Aneurophyton germanicum* Kräusel & Weyland, 1923.

### **Aneurophyton germanicum** Kräusel & Weyland, 1923

Plates 37-41

*Aneurophyton germanicum* Kräusel & Weyland, 1923, ***Beiträge zur Kenntnis der Devonflora.*** Senckenbergiana, vol. 5, pp. 154-184.

*Aneurophyton germanicum* Kräusel & Weyland, Kräusel & Weyland, 1926, ***Beiträge zur Kenntnis der Devonflora II.*** Senckenberg. Naturforsch. Ges., Abhandl., vol. 40, pp. 115-155.

*Aneurophyton germanicum* Kräusel & Weyland, Kräusel & Weyland, 1929, ***Beiträge zur Kenntnis der Devonflora III.*** Senckenberg. Naturforsch Ges., Abhandl., vol. 41, pp. 315-360.

*Species diagnosis.* — Emended by Kräusel and Weyland, 1929; here emended and amplified. Plants as described in generic diagnosis. Ultimate sterile appendages dichotomized 1-3 times, three-dimensional when forked more than once. All higher orders of sterile branch may bifurcate, some may terminate in structures comparable to ultimate appendages. Primary xylem triangular in transverse section, with rounded lobes and slightly concave sides, 1.7 mm in diameter in the n + 2 branch, one mesarch protoxylem strand near the tip of each lobe, one central. Tracheids of metaxylem scalariform and elliptical bordered pitted. Protoxylem cells 10 - 28 $\mu$m in width, those of metaxylem 28 - 56 $\mu$m. Secondary xylem of tracheids and numerous, high (up to 60 cells), uniseriate rays. Cortex consisting of more or less polygonal, large cells and strands of elongated cells. Elliptical bordered pits on all walls of tracheids, in 1 - 6 rows. Fructifications 10 mm long, consisting of central stalk that dichotomizes once to form two arms that bear short stalks 0.5 mm in length and 0.5 mm in width. Stalks inserted in two rows on each arm, each terminating in one exannulate sporangium. Sporangia average 2 mm in length, end in blunt tips, and dehisce by a longitudinal split.

*Lectotype.* — Here selected as plate 2, figure 1 of Kräusel and Weyland, 1929.

Plate 9, figures 15-17 of Kräusel and Weyland, 1923 are considered to be representative of the species.

*Material studied in present paper.* — Cornell University Paleobotanical Collection. CUPC Type Nos. 234-249, 253, 254. Illustrated are Nos. 235, 238, 240, 241, 243-246, 248, 249, 253. Not illustrated are Nos. 234, 236, 237, 239, 242, 247, 254.

*Localities of material studied.* — Pond Eddy, Sullivan Co., New York. Abandoned quarry on N. side of N.Y. State Route 97, one mile southeast of Pond Eddy along Fish Cabin Creek; small collection from Kirberg, near Elberfeld, Rhineland, Germany.

*Horizons.* — Delaware River Formation, Finger Lakes Stage, Senecan Series Upper Devonian (= Frasnian of Europe); Honseler beds, Middle Devonian, Givetian.

## DISCUSSION

*Aneurophyton germanicum* Kräusel and Weyland, 1923, is the type of Aneurophytales Kräusel and Weyland, 1941. Aneurophytales constitute the basic group of the subdivision Progymnospermopsida Beck, 1960. In recent years much has been written about this subdivision and its position with respect to the evolution of gymnosperms (*e.g.* Beck, 1976; Bonamo, 1975; papers cited therein). Nevertheless the genus *Aneurophyton* is clouded by uncertainty.

Mustafa (1975) rejected the name *Aneurophyton* because Kräusel and Weyland had placed two taxonomically different types of fructifications in *Aneurophyton* and because their specimens are now lost. Thus he believed that the genus cannot be clarified nomenclatorially. However, he found that many of Kräusel and Weyland's illustrations fit his (Mustafa's) concept of *Protopteridium* (now *Rellimia* Leclercq and Bonamo, 1973), an older name. He, therefore, suggested that most fossils earlier named *Aneurophyton germanicum* should be included in *Protopteridium* on the basis of their anatomy, histology, and morphology.

We recognize the basis for Mustafa's arguments. So did Kräusel and Weyland who (1938) removed the specimens represented by their plate 6, figures 6, 7 (1926) from *Aneurophyton* to *Protopteridium*, a change with which we concur. However, we believe that our study makes it possible to select a lectotype for *A. germanicum*. We think we have demonstrated that Kräusel and Weyland did have a plant distinct from *Rellimia* (*Protopteridium*) despite certain similarities. The morphology of the fructifications in the two genera is the most critical characteristic that distinguishes between them.

We have demonstrated by dégagement that the stalk of the fructification of *Aneurophyton* dichotomizes once only and then bears two rows of sporangia, one per stalk, on each of the upcurved arms. This is different from, and much simpler than, the pinnately branched arms of *Rellimia* (*Protopteridium*) that have been demonstrated convincingly by Leclercq and Bonamo (1971; 1973). We have found only 18 sporangia per fructification whereas in *Protopteridium* there are 250-400. Mustafa (1975) accepted Leclercq and Bonamo's description. He also recognized (p. 112) that conditions of fossilization and stage of maturity affect the appearance of fossil fructifications. We suggest that a fragment of the fructification of *Aneurophyton* can simulate a fragment of *Protopteridium*, for example text-figure 4 (left fragment) of Kräusel and Weyland (1929, p. 321). Nevertheless the two genera are distinct when relatively complete fertile parts are examined following careful uncovering. Compare, for example, our Plate 37, figures 13-15 with Leclercq and Bonamo (1971) figures 1, 9, 15, 18.

The arrangement of branches of *Aneurophyton germanicum* has also been uncertain. Kräusel and Weyland (1923) originally considered *Aneurophyton* to consist of large, planated fronds. Goldring (1924) thought the same about *Eospermatopteris*. Later the German authors (1929) suggested that the frond might be three-dimensional because they discovered a three-lobed protostele in several orders of branching. From this they suggested that *Aneurophyton* was not a typical frond. Leclercq (1940) reinforced this newer concept when she too observed its three-lobed protostele. However, until now, no one has demonstrated on the basis of gross morphology that all known orders of branching, both sterile and fertile, are produced in spiral fashion as had been predicted from anatomy. Our demonstration of spiral arrangement and the repetitive anatomical pattern in all orders of branching (Kräusel and Weyland, 1929) show that *Aneurophyton* is a branching system and not a stem bearing fronds. Carluccio, Hueber, and Banks (1966) demonstrated on similar evidence that *Archaeopteris* bears a system of lateral branches, not fronds. We still do not know if ultimate appendages of *Aneurophyton* are vascularized but we are willing to predict that they will be shown to have small traces different in shape from the three-lobed protostele of the penultimate branch on which they are borne. In our material ultimate appendages are forked no more than two times although Kräusel and Weyland (1926) illustrated 1-3 dichotomies in their text-figure 9. The ultimate appendages of the Cornell specimens appear to be three-dimensional, not planated, when they dichotomize twice. These appendages if planated and webbed would be equivalent to the leaves of *Archaeopteris*. In *Aneurophyton* they can be interpreted as precursors of leaves.

Variation in the gross appearance of fructifications of *Aneurophyton germanicum* has added to the confusion surrounding the genus. Why do the arms of the fructification sometimes appear to bear sporangia directed away from (typical) or sometimes directed toward (atypical) the penultimate branch (contrast Pl. 37, figs. 13, 15 with Pl. 39, figs. 16, 19)? This same apparent discrepancy appears in the illustrations of Kräusel and Weyland (1929, text-fig. 6, typical; text-fig. 2, atypical) and in Stockmans' (1948) illustrations of *Aneurophyton olnense* (see his pl. 3, fig. 4, typical fructification nearest left margin; pl. 3, fig. 1, atypical fructification at proximal end of second penultimate on right). We suggest that during the life of the plant there was only one kind of fructification. The second is an artifact of preservation. The following hypothesis is proposed. During transport by water some parts of the plant were softened. Because of the spiral arrangement, two out of every three fructifications lay more or less parallel to the bedding plane when deposition occurred. The third was directed perpendicular to that plane. To be preserved in its natural position this fructification would have to remain upright during the continual raining down of sediment. More likely its stalk began to bend until it doubled over in contact with itself. In such a position one would find a fructification apparently with a short stalk and an inverted lyre-shaped structure, hence the fructification we are calling atypical.

Two features of the paleoenvironment contribute to the feasibility of this hypothesis. The fossil locality at Pond Eddy is part of a continental deposit. Fining-upward cycles indicate not only the fluvial nature of the deposit but also that the nature of the river continually changed. Gentle flow carried and deposited clay particles only. Rapid flow transported particles of many sizes but deposited only those of sand size (Blatt, Middleton, and Murray, 1972, chapt. 4, 6). Transportation by such a river system would contribute to both the softening and the twisting of the plant fragments. The plant material was clearly transported some distance from the site where it grew. Utilizing paleocurrents and fold patterns Fletcher and Woodrow (1970) hypothesized that the source of the sediment comprising the Delaware River Formation was southeast of Milford, Pennsylvania. This means that the plant fragments were transported at least 17.6 km to Pond Eddy, New York, allowing ample opportunity for reorientation of the structure and subsequent appearance of the fructifications.

Anatomical structure in *Aneurophyton germanicum* is less confusing, perhaps because it needs more detailed study. Kräusel and Weyland (1929) reported a triangular protostele in $n + 1$, $n + 2$, and penultimate branches. They described three mesarch protoxylem strands, one near the apex of each arm. Leclercq (1940) reported a fourth, centrally located. We have confirmed both the triangular protostele and four protoxylem strands. We have also shown some detail of the formation of branch traces. Below the separation of a penultimate branch a protoxylem strand elongates radially, then divides leaving two strands along a radius. Simultaneously the apex of the arm enlarges, a constriction appears below the enlargement, and finally the enlargement is separated from the parent lobe as a branch trace. Presumably it soon becomes three-lobed and by division of its protoxylem strand develops the typical complement of four protoxylem strands. Some of this development is illustrated (Pl. 40, figs. 23-25; Pl. 41, figs. 26, 27). There is no evidence of parenchyma in the primary xylem. Further, we have no evidence nor do we know of any published evidence of more than four protoxylem strands in any order of branching. We have contributed nothing to the still open question of vascular tissue in ultimate appendages. Secondary xylem is characteristic of Aneurophytales (Beck, 1957; Matten and Banks, 1966; Scheckler and Banks, 1971a) with its high, uniseriate vascular rays and tracheids with multiseriate elliptical bordered pits on all walls.

A final source of confusion is that *Aneurophyton germanicum* lacks a holotype. Valid publication prior to 1958 did not require such a type. Following Art. 7 of the I.C.B.N. (Stafleu, *et al.*, 1972) we designate plate 2, figure 1 (see also note 1 of Art. 9) of Kräusel and Weyland (1929) as the lectotype. We consider plate 9, figures 15-17 of Kräusel and Weyland (1923) to be representative of the genus and species. So far as we can learn (including oral communication between the late Dr. Kräusel and the present junior author) most of the collection of Kräusel and Weyland was destroyed during World War II. The rationale for selecting a lectotype rather than a neotype is that the former is an element the authors had in hand and it was well illustrated. Similar specimens have been seen in *A. olnense* (Stockmans, 1948) and in the present material from New York. It seems unnecessary to select a neotype. Should any original material be rediscovered it would then be used as type (Stafleu, *et al.*, 1972; note 4f. — *Guide for the determination of types*).

We assign the New York fossils to *Aneurophyton germanicum* Kräusel and Weyland, 1923, because they agree in anatomical and morphological detail with the German material. Both exhibit a three-lobed, mesarch protostele, ultimate appendages apparently with no vascular strand, dichotomous forking of n + 2 branches, dichotomizing ultimate appendages, lyre-shaped fructifications, sporangia borne singly on short stalks on the two arms of the fructification, and some atypical fructifications. Minor variations found in the New York specimens are the fourth, central protoxylem strand, two but not three, forks on the ultimate appendages, dichotomies of the penultimate as well as n + 2 branches, and Frasnian rather than Givetian age. These variations are insufficient to warrant the description of a new species. The age difference we treat as an extension of the range of the species from Middle into Upper Devonian strata. But the German specimens are late Givetian and the American are early Frasnian so that the difference is not so much as the loosely used terms Middle and Upper Devonian imply.

In view of the limited study that fructifications of the German collections have received and of the varied and sometimes fragmentary manner in which they are preserved, we are fortunate to have had available for study a few specimens from the type area. One of these, illustrated in Plate 38, figure 14, shows a typical lyre-shaped fructification similar to those we have described from New York. Although a reexamination of good new collections from Germany is still necessary, our specimens from New York are similar enough to those we have from Germany to convince us that we are dealing with one plant from two widely separated localities.

We rejected *Aneurophyton erianum* (Dawson), Goldring, 1924, as a name for our material because its fructification and anatomical structure are unknown and its sterile branching system is composed of discordant elements. Skog and Banks (1973) showed Goldring's (1924) text-figure 3 to be *Ibyka amphikoma* Skog and Banks, 1973. We suggest that Goldring's text-figure 4 is probably *Tetraxylopteris schmidtii* Beck, 1957, because of its opposite, decussate branching pattern. Until the few remaining specimens of branch system described by her are somehow restudied, or new ones found, the species *A. erianum* is of dubious merit. The unattached, paired, terminal sporangia described by Goldring (1924) as seeds show no characteristics of *Aneurophyton.*

Our use of the name *Aneurophyton germanicum* requires that we compare Mustafa's and our opinion of the illustrations provided in Kräusel and Weyland's three papers. These are given in Table 1.

Our study suggests that Mustafa (1975) placed structures into *Rellimia* (*Protopteridium*) that clearly differ from that taxon as redefined by Leclercq and Bonamo (1971; 1973). For example we agree with Mustafa that Kräusel and Weyland (1926) illustrated *Rellimia* (*Protopteridium*) in their plate 6, figure 6. We think it clear, however, that plate 9, figures 15-17 of Kräusel and Weyland (1923) represent a far simpler fructification that does not fit the description of *Rellimia* but that does fit our concept of *Aneurophyton.*

In a similar way Mustafa (1975) may have illustrated the anatomy of two different taxa under the name *Protopteridium.* For example, his plate 14, figures 5, 6 and plate 15, figure 1, resemble the anatomy of the form genus *Cairoa* Matten, 1973. They may be *Rellimia* (*Protopteridium*). His plate 16, figure 1 resembles our concept of *Aneurophyton* as both Leclercq (1940) and we have illustrated it. It would be necessary to obtain permineralized fragments from several orders of branching on one complete frond to know whether or not the number of protoxylem strands changes in the different orders.

We summarize in Table 2 the major differences between *Rellimia* Leclercq and Bonamo, 1973 (*Protopteridium*) and *Aneurophyton* as we perceive them.

Among Aneurophytales the position of *Aneurophyton* as the most primitive member now seems assured. Its fructification is the least branched followed by *Triloboxylon* (Scheckler, 1975), *Rellimia* (Leclercq and Bonamo, 1971) and *Tetraxylopteris* (Bonamo and Banks, 1967) in a series of increasing complexity. The first three genera are branched spirally whereas *Tetraxylopteris,* whose fructification is the most complex, is opposite decussate. Anatomically, *Aneurophyton* is the least complex with four protoxylem strands and tracheids only. *Triloboxylon* has a larger protostele and 18-22 protoxylem strands, some parenchyma, and a band of narrow tracheids joining the protoxylem strands (Matten and Banks, 1966; Scheckler and Banks, 1971a). The anatomy of *Rellimia* is still poorly known. It appears to have an irregular three-lobed protostele (Kräusel and Weyland,

Table 1. Comparison of the interpretation by Mustafa (1975) and Serlin and Banks of the figures published by Kräusel and Weyland (1923, 1926, 1929).

| | |
|---|---|
| | Kräusel and Weyland, 1923 |
| Mustafa (1975) placed the following in *Protopteridium*: | Serlin and Banks |
| plate 8, figures 6-12<br>plate 9, figures 14-17 | Of these and the few other illustrations in this paper we give a name only to figures 15-17 on plate 9. These are fertile *Aneurophyton*. |
| | Kräusel and Weyland, 1926 |
| Mustafa placed in *Protopteridium*: | Serlin and Banks |
| plate 6, figure 6<br>plate 6, figure 7 | Of these two figures we would name only figure 6 and agree that it is *Rellimia (Protopteridium)*.<br>Mustafa omitted mention of plate 7, figures 1-4 all of which may be sterile *Aneurophyton*.<br>Other illustrations in the paper are of anatomy or of unattached axes for which we have too little evidence to make an identification.<br>Text-figure 9 is a drawing of a sterile frond of *Aneurophyton* which we accept although it should be drawn as a three-dimensional structure. Text-figures 10, 11a, and 11b are rough sketches of a fertile frond and fructifications that fit our concept of *Aneurophyton*. |
| | Kräusel and Weyland, 1929 |
| Mustafa placed in *Protopteridium*: | Serlin and Banks |
| plate 2, figures 1-5 | Of these figure 1 is our lectotype of *A. germanicum;* figures 2-4 we do not name; figure 5 we call *Tetraxylopteris*. |
| plate 3, figures 6-8 | These may be anatomy of *Aneurophyton*.<br>Plate 3, figures 1-5 are not mentioned by Mustafa and we are uncertain of their affinity; they could be sporangia of *A. germanicum*. |
| plate 4, figures 1-7 | We suggest that these show anatomy of *Aneurophyton* as Kr. & W. said. |
| plate 5, figures 1-5 | Also anatomy of *Aneurophyton*<br>Text-figure 2 is fructification of *Aneurophyton;* 3 is a broken fructification; 4 is a poorly drawn fructification; 5 is one-half of a fructification; 6 is a whole fructification; 7 is one sporangium; all can be *Aneurophyton*. |

1938), but we wonder if after further study, it will prove, to be more like that of *Cairoa* or *Triloboxylon*. *Tetraxylopteris* (Beck, 1957; Scheckler and Banks, 1971a) has a four-lobed protostele composed of tracheids and parenchyma, and 30 protoxylem strands. At certain levels it has a mixed pith which leads to the suggestion that *Tetraxylopteris* illustrates a stage in the derivation of a siphonostele from a protostele. *Tetraxylopteris* is structurally the most complex genus of the order.

Table 2. Comparison of *Rellimia (Protopteridium)* and *Aneurophyton*.

| | *Rellimia (Protopteridium)* | *Aneurophyton* |
|---|---|---|
| Diameter of branches and number of protoxylem strands | | |
| 1st order or n + 1 | up to 2.5 cm<br>to 9 protoxylems | 4.0 mm<br>px not known |
| 2nd order or n + 2 | 2.5 mm<br>6-9 protoxylems | 2.0 mm<br>4 protoxylems |
| 3rd order or penultimates | 1.5 mm<br>3-6 protoxylems | 1.5 mm<br>px not known |
| 4th order when present | 1.0 mm<br>not found | 1.2 mm<br>not found |
| Fructification | | |
| | whole structure curved adaxially | two arms curve toward one another, lyre-shaped |
| | whole structure 1-4 cm high | whole structure about 1 cm long |
| | structure once dichotomized, then branched pinnately | structure once dichotomized only |
| | 250-400 sporangia<br>sporangia 3.5 mm long (Leclercq and Bonamo, 1971) or 5.5-7.0 mm long (Mustafa, 1975) | 18 sporangia<br>sporangia 2.0 mm long |
| | sporangia linear with an apiculate tip | sporangia elliptical-oblong, blunt tipped |
| | spores-*Rhabdosporites langii* (Eisenack), Richardson, 1960 | spores-*Aneurospora goensis* Streel, 1964 |
| Ultimate appendages | | |
| | twice or three times dichotomized, tips apparently not recurved | once to three times dichotomized, not planated, tips recurved to varying degrees |
| | total length perhaps 7-8 mm | total length 4-5 mm |

Based on their anatomy only *Cairoa* (Matten, 1973) and *Proteokalon* (Scheckler and Banks, 1971b) have been assigned tentatively to Aneurophytales. The shape of their protostele changes from one order of branching to another indicating a degree of anatomical complexity. In *Cairoa* a three-lobed strand is found in n + 2 axes, a diamond-shaped strand in penultimate branches. It has no parenchyma and has six protoxylem strands in n + 2 axes. *Proteokalon* Scheckler and Banks, 1971b, has a skewed four-lobed protostele that becomes three-lobed in branches. Protoxylem strands vary from 4 - 36 and some parenchyma is found in the metaxylem. Where known, ultimate appendages in Aneurophytales are supplied by terete traces. Barnard and Long (1975) suggested that those aneurophytes whose anatomy is repeated in all except ultimate branches constitute one evolutionary line and those whose anatomy changes in different orders constitute another. However, the morphology of *Cairoa* and *Proteokalon* must be learned before this suggestion can be developed in detail.

The concept of Progymnospermopsida as a group intermediate between trimerophytes and gymnosperms has made extensive progress since its inception 17 years ago (Beck, 1976; Bonamo, 1975). Many more detailed studies are needed in order to establish whole plants from these several fairly well-described branching systems. For example, the main axis and hence the habit of *Aneurophyton* are completely unknown. Its association at several localities with tree stumps called *Eospermatopteris* may be significant or it may be only coincidental. One can only hope for a fortuitous quarrying operation to make available the missing data.

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# PLATES

## EXPLANATION OF PLATE 37

| *Figure* | | *Page* |
|---|---|---|
| 1-7. | *Aneurophyton germanicum* Kräusel and Weyland | 347 |

1. n + 1 axis bearing ten n + 2 branches ( A - J) attached spirally. CUPC Type, No. 245.1-3; × 2/3.

2. Counterpart of portion of specimen illustrated in figure 1. The length of n + 1 axis (ax) seen here fills the apparent gap in the n + axis on figure 1 between the point of attachment of branch B and the point indicated by line D. Branch D, not seen on figure 1, is seen here. The counterpart of n + 2 branch B is also seen here. CUPC Type, No. 245.5; × 1.4.

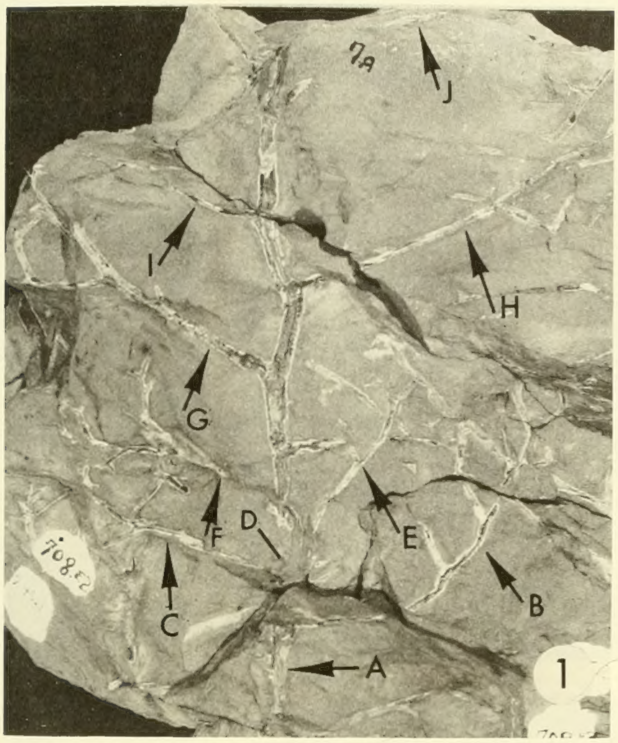
3. Enlargement of branch F from figure 1. This n + 2 branch bears two penultimate appendages (1,2). Penultimate branch 1 bears two ultimate appendages (u). Branch 2 bears only the bases of two ultimate appendages. CUPC Type, No. 245.1; × 1.6.

4. An n + 2 branch that bears six penultimate branches (1 - 6) in spiral order. Two ultimate appendages (u) are indicated on penultimate branch 4. The n + 2 branch has dichotomized (d). Penultimate branches (p) and portions of ultimates are found on the right arm of the dichotomy as well as on the left. CUPC Type, No. 246; × 1.5.

5. Penultimate branch (p) has undergone a dichotomy. Ultimate appendages are seen on both arms. Several (one indicated by arrow) show two dichotomies. CUPC Type, No. 243.1; × 1.5.

6. Ultimate appendage indicated by arrow in figure 5. Right arm of first dichotomy bends down. Arms of second dichotomy spread out in plane of matrix. CUPC Type, No. 243.1; × 6.

7. A penultimate branch that bears two ultimate appendages. CUPC Type, No. 246; × 2.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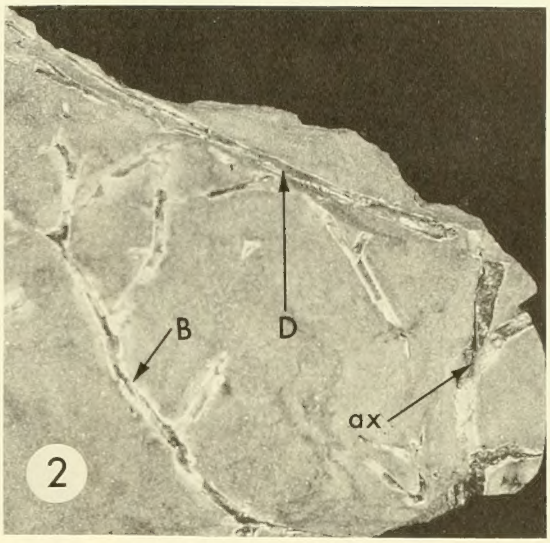
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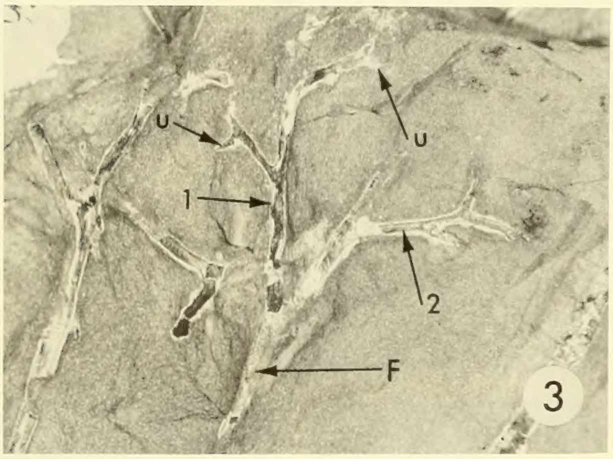
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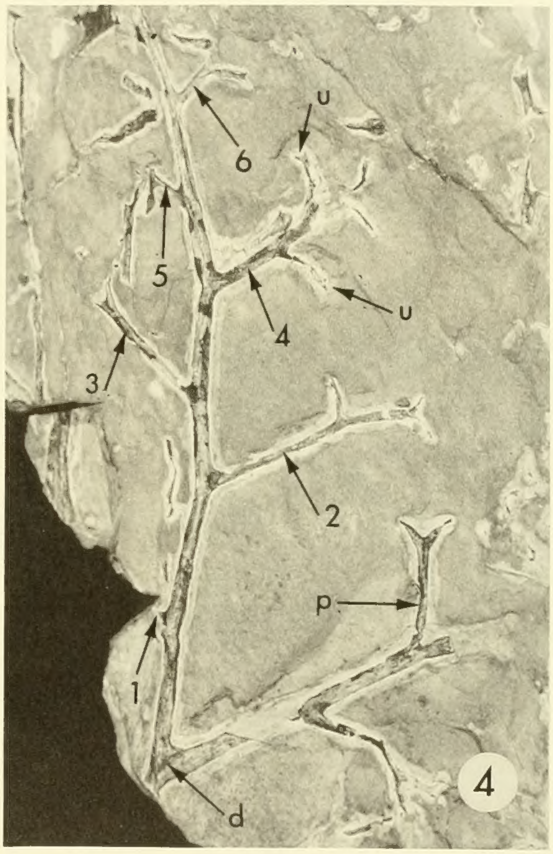
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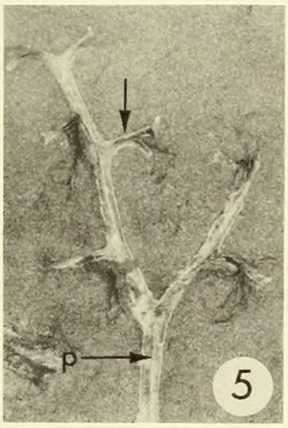
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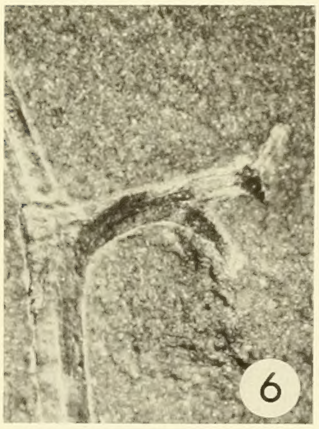
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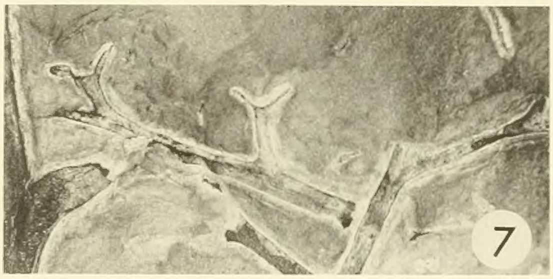
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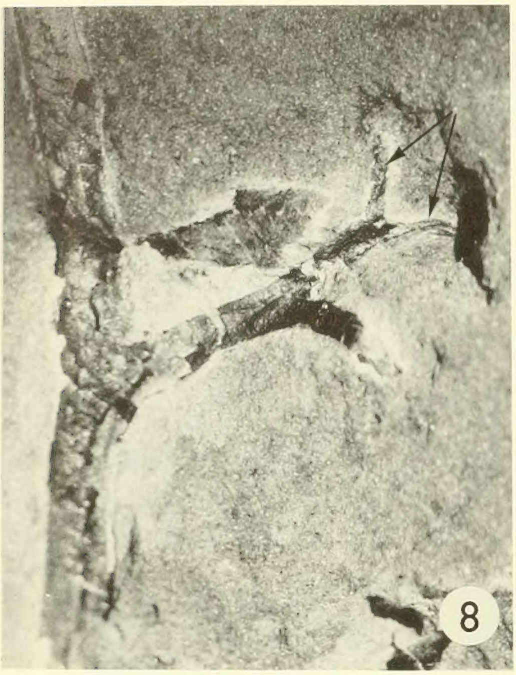
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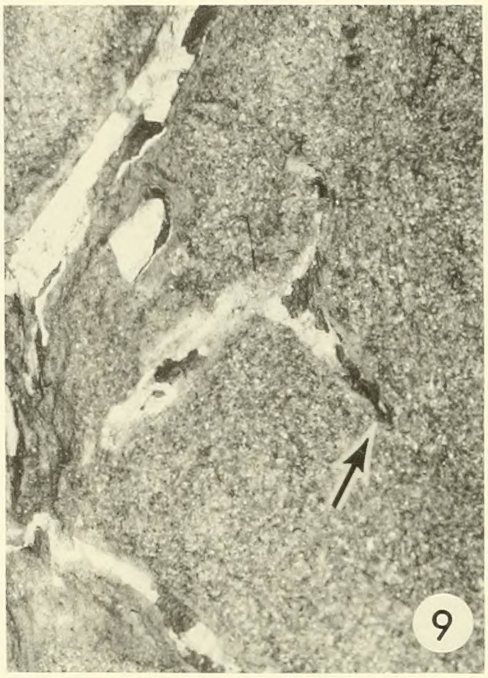
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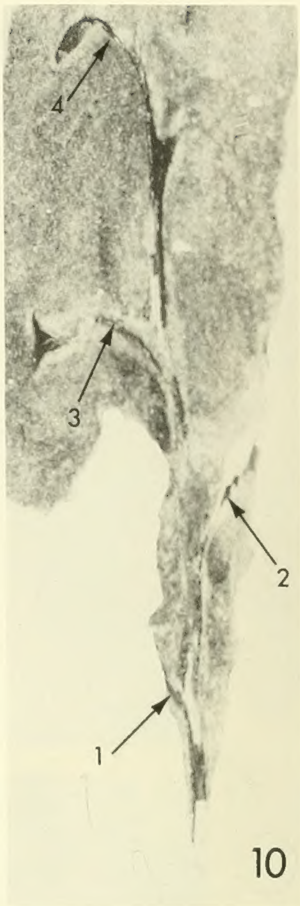

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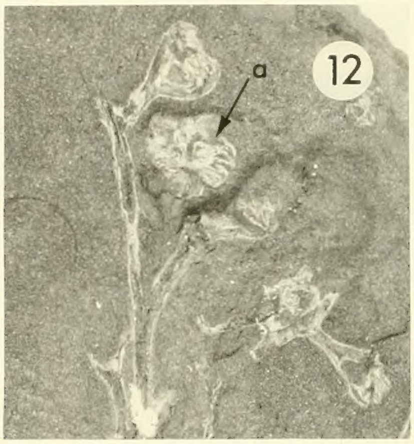

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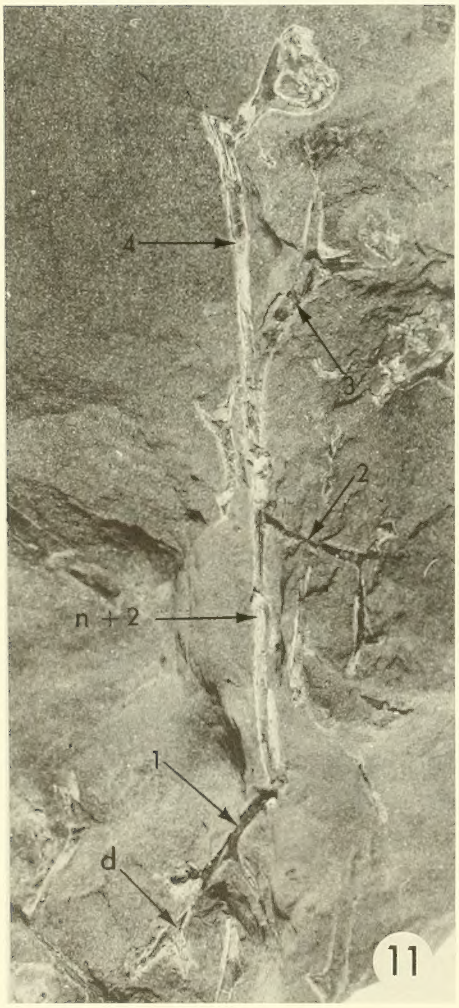

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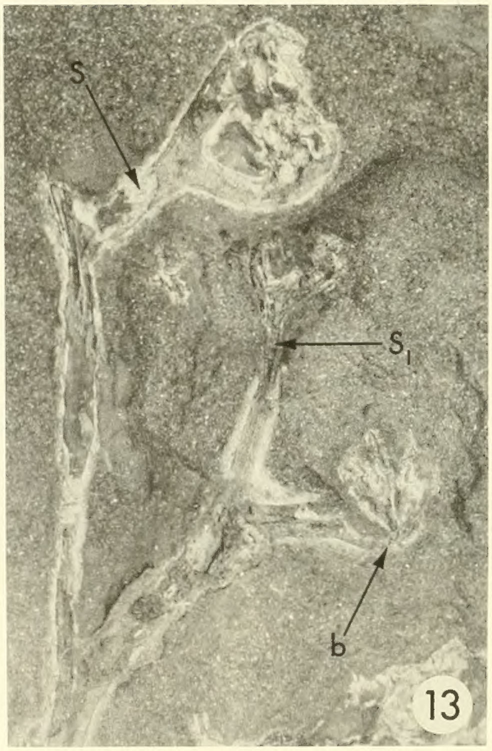

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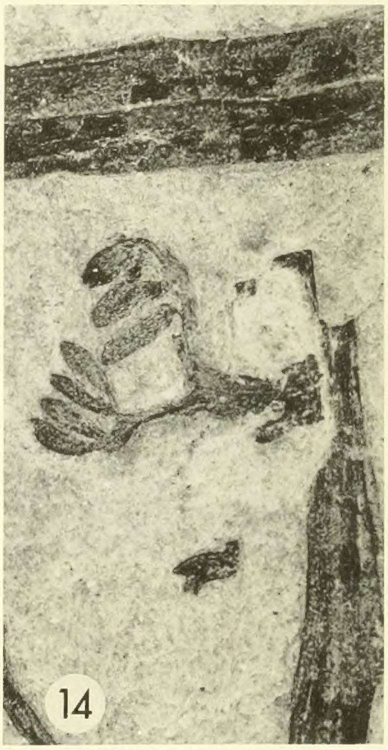
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## EXPLANATION OF PLATE 38

*Figure* *Page*

8-14. *Aneurophyton germanicum* Kräusel and Weyland .......... 347

8. An ultimate appendage. One arm has undergone a second dichotomy resulting in two more tips (arrows). The right arm of first dichotomy bends up whereas the two arms of second dichotomy are in the plane of the matrix. CUPC Type, No. 235; × 9.

9. An ultimate appendage whose arms spread apart horizontally and taper to pointed apices (one indicated by arrow). CUPC Type, No. 238.1; × 6.

10. Penultimate branch bearing four ultimate appendages (1 - 4) in spiral order. CUPC Type, No. 248.2; × 3.

11. n + 2 branch that bears four penultimates (1 - 4) in spiral order. Penultimate branch 1 has dichotomized (d). CUPC Type, No. 244; × 1.8.

12. Upper part of specimen shown in figure 11 prior to dégagement of a fructification (a) that is seen flattened in face view. The fructification above it, seen in side view, is lyre-shaped. CUPC Type, No. 244; × 1.

13. Enlargement of upper portion of specimen seen in figure 11 following dégagement of fructification indicated by a in figure 12. The stalk of the fructification ($S_1$) has been uncovered by removal of sporangia. A second fructification (b) is attached to the same penultimate branch. Arrow S indicates the central stalk of typical lyre-shaped fructification. CUPC Type, No. 244; × 3.8.

14. Lyre-shaped fructification on specimen collected at or near type locality in Germany. CUPC Type, No. 253; × 5.6.

## EXPLANATION OF PLATE 39

| *Figure* | | *Page* |
|---|---|---|
| 15-19. | *Aneurophyton germanicum* Kräusel and Weyland | 347 |

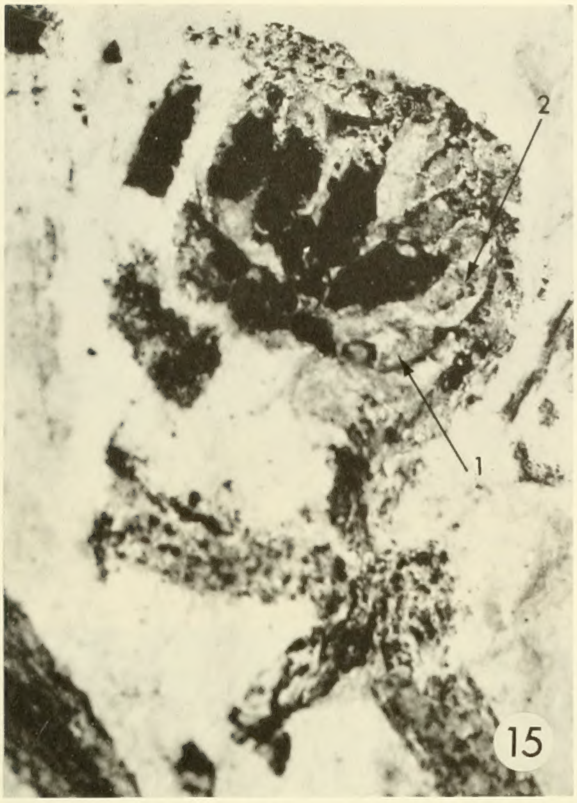
15. A typical fructification. The right arm and the basal portion of the left are intact. They bend up and in. Sporangia are arranged in two rows; number 1 is in one row, number 2 is in a second row. These two sporangia are relatively clear of coaly matter, the others are black. CUPC Type, No. 238; × ca. 10.

16. An atypical fructification. The stalk appears to dichotomize as usual but the arms of the dichotomy bearing sporangia bend down (in contrast to the bending seen in fig. 15). S — stalk of fructification. CUPC Type, No. 249; × 10.

17. Gross view of a fertile branch system. Arrow indicates the area where subsequent dégagement revealed a fructification. See also figure 18 and 19 which, with 17, constitute a series. CUPC Type, No. 240; × 4/5.

18. Enlargement of a portion of figure 17 that was indicated by arrow. S indicates basal portion of central stalk. Arrows b and c indicate the arms of the lyre that bend down. CUPC Type, No. 240; × 4.6.

19. Atypical fructification revealed after the dégagement of the specimen illustrated in figure 18 was completed. Arrow S indicates the distal portion of the central stalk that remains after dégagement. The stalk of one sporangium is indicated by st. That sporangium and the one next to it suggest that there are two rows of sporangia. CUPC Type, No. 240; × 17.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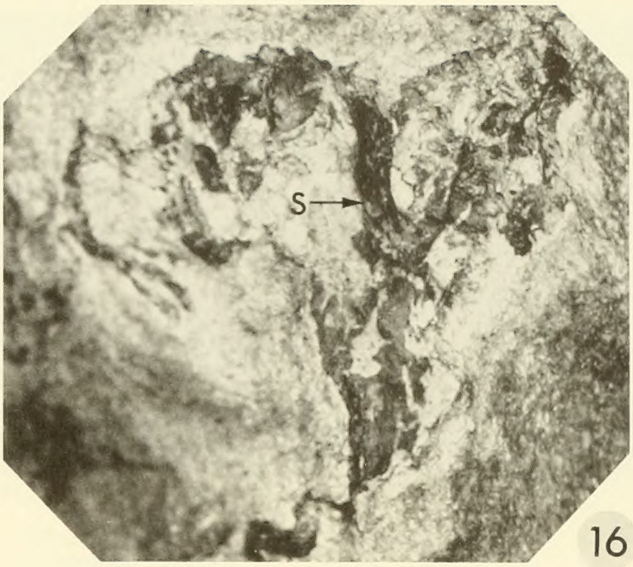
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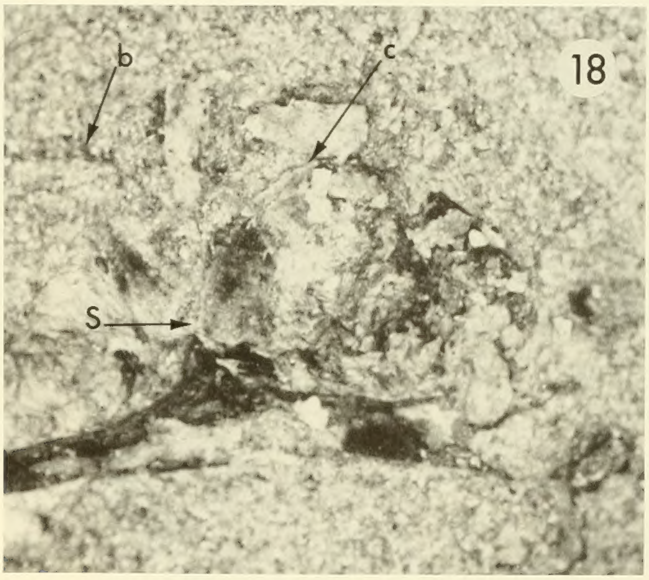
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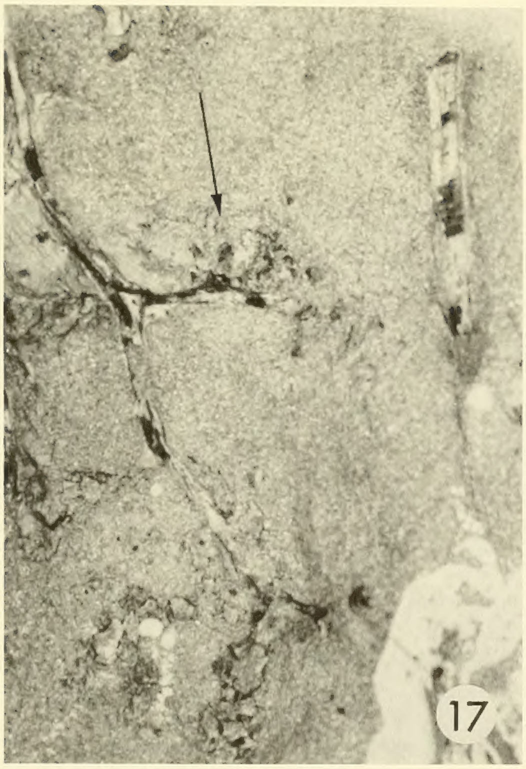
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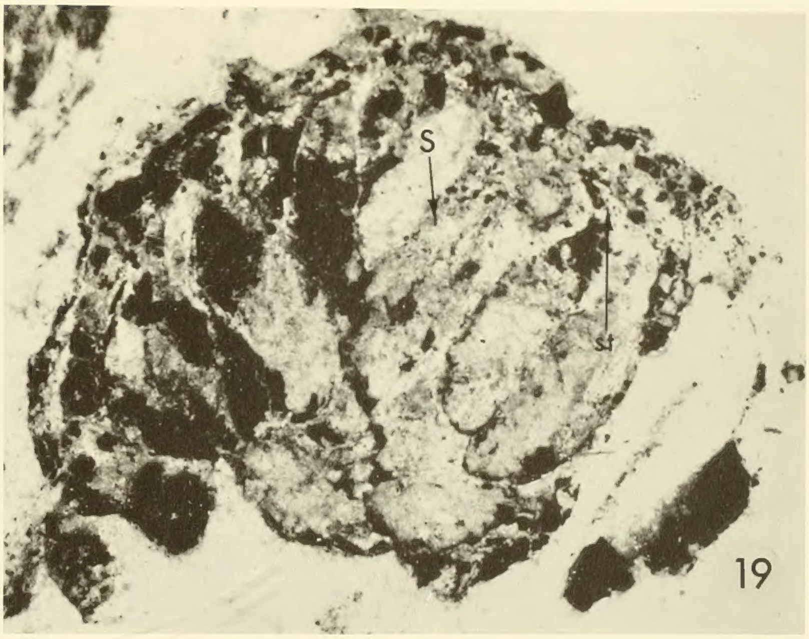
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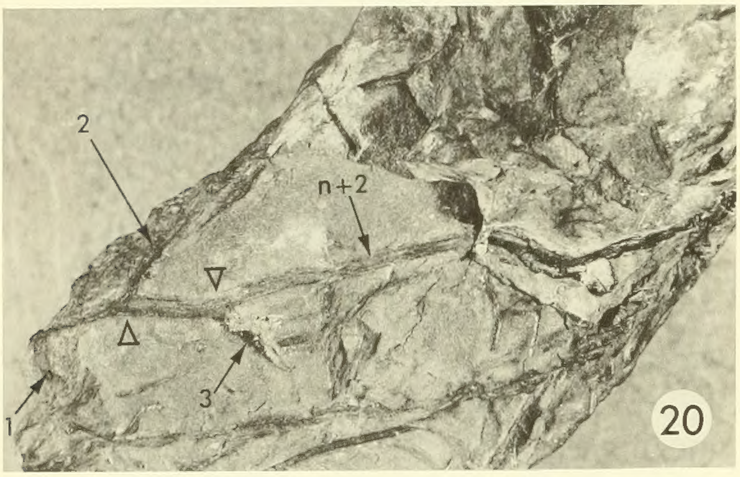

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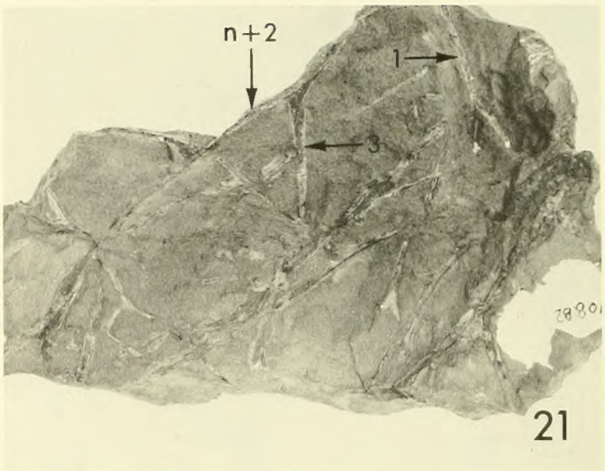

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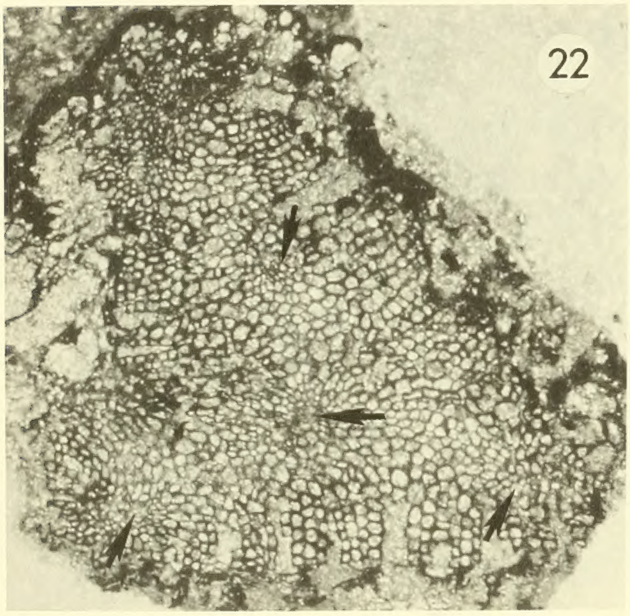

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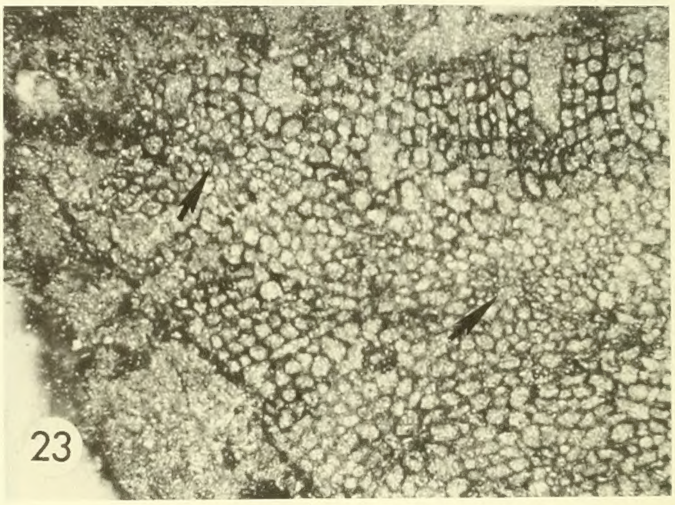

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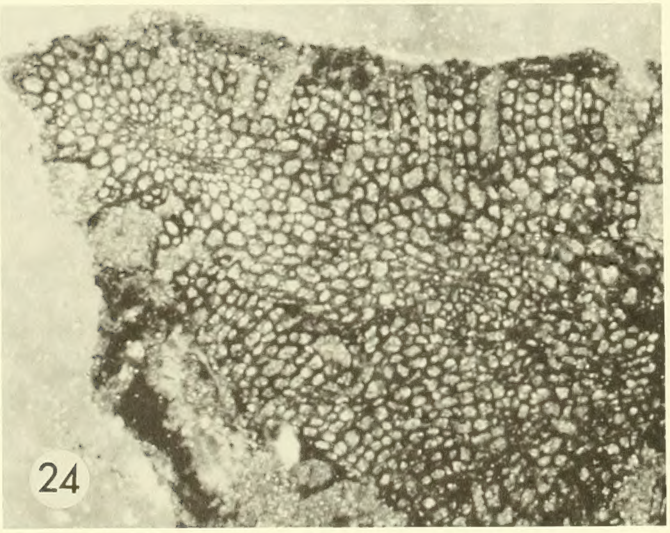

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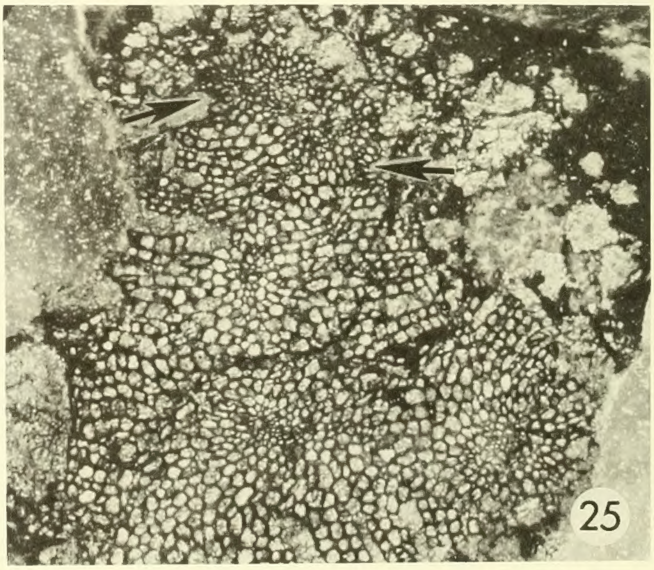

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## EXPLANATION OF PLATE 40

| *Figure* | | *Page* |
|---|---|---|
| 20-25. | *Aneurophyton germanicum* Kräusel and Weyland | 347 |

20. n + 2 axis bearing three penultimate branches (1 - 3). Δ's indicate limits of pyritized n + 2 that was removed and sectioned for anatomy. CUPC Type, No. 241.1; × 2/3.

21. Counterpart of specimen in figure 20. Note n + 2 and penultimate branches 1 and 3. Branch 1 is more complete here than in figure 20. It passes through this specimen and on the reverse side (not illustrated) it bears an ultimate appendage. CUPC Type, No. 241.2; × 2/3.

22. Transverse section of n + 2 axis. Xylem is three-lobed and has four mesarch protoxylem strands (arrows). Some secondary xylem present. CUPC Type, No. 241.1, slide, No. 31; × 42.

23. One lobe of xylem enlarged. Section taken below level at which branch formation has begun. Note single protoxylem strand near apex of lobe (arrow). Central protoxylem also seen (arrow). CUPC Type, No. 241.1, slide, No. 17; × 82.

24. Section of same lobe as in figure 23 at a higher level. Both the lobe and its protoxylem are elongated in a radial direction. CUPC Type, No. 241.1, slide, No. 18; × 86.

25. Branch trace (arrows) almost free from lobe. One half of the elongate protoxylem strand seen in figure 24 remains in parent lobe following division. CUPC Type, No. 241.1, slide, No. 30; × 65.

## EXPLANATION OF PLATE 41

| Figure | | Page |
|---|---|---|
| 26-30. | *Aneurophyton germanicum* Kräusel and Weyland | 347 |

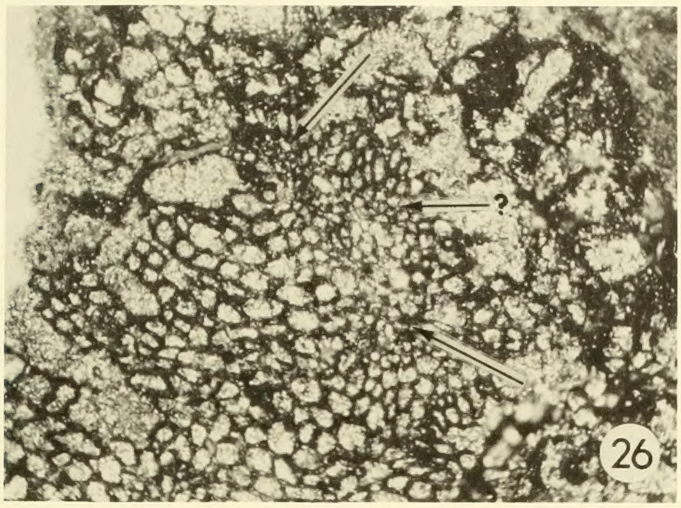
26. Branch trace from figure 25 enlarged. Two or possibly three protoxylem strands are visible (arrows). CUPC Type, No. 241.1, slide, No. 30; × 112.

27. Same branch trace at a higher level. It is almost triangular in outline and shows at least three protoxylem strands (arrows). CUPC Type, No. 241.1, slide, No. 32; × 120.

28. Radial section of secondary xylem showing procumbent ray cells with relatively thin walls. CUPC Type, No. 241.1, slide, No. AR; × 280.

29. Tangential section of secondary xylem showing high, uniseriate rays. CUPC Type, No. 241.1, slide, No. AL; × 98.

30. Radial section of secondary xylem showing multiseriate elliptical bordered pits on tracheid walls. CUPC Type, No. 241.1, slide, No. AL2; × 580.



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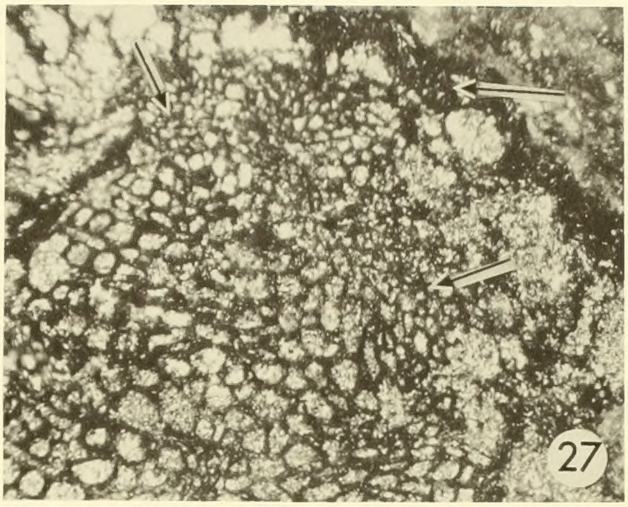

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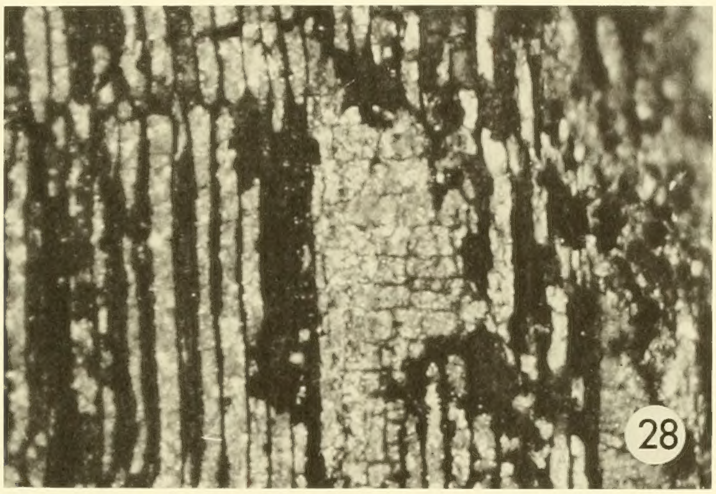

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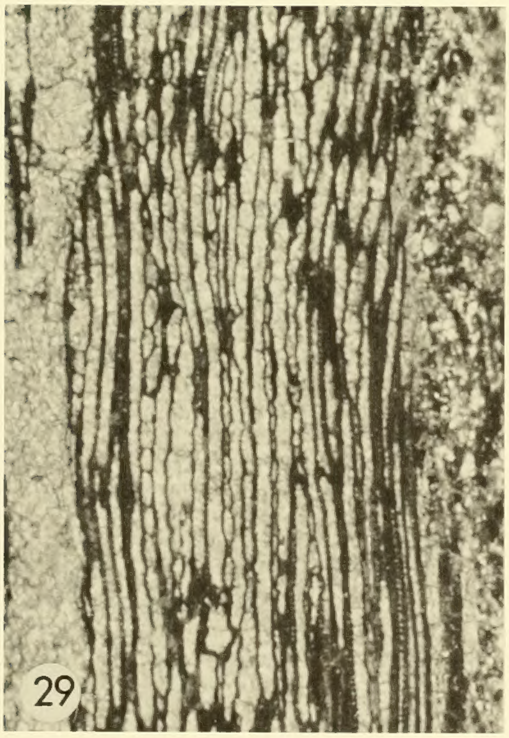

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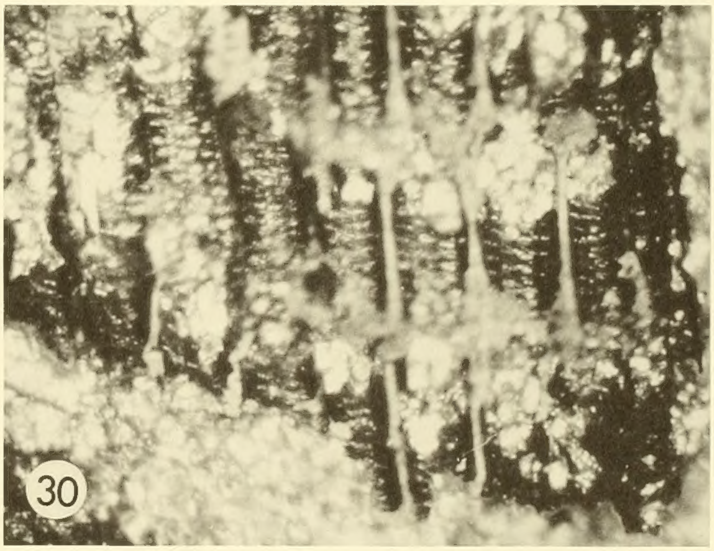

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